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Modelling temperature-dependent larval development and subsequent demographic Allee effects in adult populations of the alpine butterfly Parnassius smintheus

by

Jeanette D. Wheeler, C.J. Bampfylde, M.A. Lewis

UNIVERSITY OF OXFORD

Oxford Centre for Collaborative Applied Mathematics
Mathematical Institute
24 - 29 St Giles'
Oxford
OX1 3LB
England

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Abstract Climate change has been attributed as a driver of changes to ecological systems worldwide and understanding the effects of climate change at individual, population, community, and ecosystem levels has become a primary concern of ecology. One avenue toward understanding the impacts of climate change on an ecosystem is through the study of environmentally sensitive species. Butterflies are sensitive to climatic changes due to their reliance on environmental cues such as temperature and photoperiod, which regulate the completion of life history stages. As such, the population dynamics of butterflies may offer insight into the impacts of climate change on the health of an ecosystem. In this paper we study the effects of rearing temperature on the alpine butterfly *Parnassius smintheus* (Rocky Mountain Apollo), both directly through individual phenological changes and indirectly through adult reproductive success at the population level. Our approach is to formulate a mathematical model of individual development parameterized by experimental data and link larval development to adult reproductive success. A Bernoulli process model describes temperature-dependent larval phenology, and a system of ordinary differential equations is used to study impacts on reproductive success. The phenological model takes field temperature data as its input and predicts

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Jeanette D. Wheeler
Centre for Mathematical Biology, Department of Mathematical and Statistical Sciences, University of Alberta, Edmonton, Alberta, T6G 2G1, Canada
E-mail: jdwhe@mit.edu
Present address: Woods Hole Oceanographic Institution, 266 Woods Hole Rd., MS# 34, Woods Hole, MA, 02543-1050

C.J. Bamfylde
Clean Energy Policy Branch, Policy Division, Alberta Environment, Government of Alberta, 12th Floor Baker Centre, 10025 106 St., Edmonton, Alberta, T5J 1G4, Canada

M.A. Lewis
Centre for Mathematical Biology, Department of Mathematical and Statistical Sciences, and Department of Biological Sciences, University of Alberta, Edmonton, Alberta, T6G 2G1, Canada

a temporal distribution of adult emergence, which in turn controls the dynamics of the reproductive success model. We find that warmer spring and summer temperatures increase reproductive success, while cooler temperatures exacerbate a demographic Allee effect, suggesting that observed yearly fluctuations in *P. smintheus* population size may be driven by inter-annual temperature variability. Model predictions are validated against mark-recapture field data from 2001 and 2003 – 2009.

Keywords *Parnassius smintheus*, · Allee effect, · phenology, · population dynamics, · climate change

1 Introduction

Since the late twentieth century, climate change has been attributed as a major driver of changes to ecological systems worldwide (IPCC, 2007). Understanding the effects of climate change at individual, population, community, and ecosystem levels has since become a primary area of research in ecology (Parmesan, 2006). Changes to climatic variables can affect species in empirically detectable ways. For instance, at an individual level, temperature changes can influence developmental rate, body size, and egg production in ectotherms (Taylor, 1981; Atkinson, 1994; Gibbs et al, 2010). At a population level, temperature changes can impact timing of life history events (Post et al, 2001), and at a community level, the shift in time of such life history events (such as egg hatching, adult emergence, and flowering) can remove or alter the temporal overlap of previously interacting species (most common in predator-prey and insect-host plant interactions, as discussed in Visser and Both (2005)).

Impacts of climate change have long been studied through indicator species like insects (reviewed in Parmesan (2006)). Insects, and butterflies in particular, are especially sensitive to climatic changes due to their reliance on environmental cues such as temperature and photoperiod to complete stages of their life history (Taylor, 1981). Butterflies make excellent study species when considering climatic effects as data sets for certain species extend back as far as 100 years, enabling the study of the influences of long-term climatic shifts (Parmesan et al, 1999). Further, many species may be reared experimentally to determine temperature effects on larval growth or body size (see Taylor, 1981; Atkinson, 1994). These effects are often understood in a “normal” temperature range, but the future climatic changes predicted by global climate models may challenge this understanding of temperature-dependent dynamics. Climate change may present threats to species persistence through multiple mechanisms which include: habitat fragmentation and range shifts (Hill et al, 1999; Parmesan et al, 1999), and changing phenology, which may impact a population by way of trophic mismatches (Thomson et al, 2010; Schweiger et al, 2008; Hoye and Forchhammer, 2008; Both et al, 2009), temporal overlap with new predators or parasites (Thomson et al, 2010), and density-regulated activities such as successfully attacking resources (Berryman et al, 1985) and mate-finding (Calabrese and Fagan, 2004; Calabrese et al, 2008).

Perhaps most significantly, individual development time must coincide with resource availability, a consideration especially important for specialist herbivores and pollinators (Yurk and Powell, 2009). In the worst-case scenario, a host plant or other necessary resource cannot persist within a changing temperature regime, which results in habitat fragmentation for the insect species under consideration (Stork et al, 2009; Schweiger et al, 2008). Habitat fragmentation and contraction is especially dangerous for species that are geographically isolated or have barriers to dispersal, such as mountainous species (Parmesan, 2006). Resources need not be absent from a habitat, however, to make them unavailable. Trophic mismatches can occur when the seasonal temporal overlap of a resource and its consumer are influenced by climatic changes (documented in Lepidoptera *Epiphyas postvittana*, *Boloria titania*, the *Nymphalidae* family, and *Operophtera brumata* and *Tortrix virirdana* in Thomson et al (2010); Schweiger et al (2008); Hoye and Forchhammer (2008); Both et al (2009), respectively). Thus, understanding how climate drives developmental rate change in insects is important for species conservation.

The survival of a species may hinge on its response to climatic shifts, and mathematical modelling provides a tool which may allow the prediction of species persistence. Given a temperature-varying experiment documenting larval growth rates in a small population, a mathematical model may be parameterized which allows the exploration of multiple climatic scenarios as well as indirect effects of temperature change that cannot be observed by the initial experiment.

In this study, the effects of temperature on development time, phenology, and adult reproductive success are considered for the alpine butterfly *Parnassius smintheus* (Rocky Mountain Apollo). Found in alpine meadows in Western Canada and the United States, some populations are under potential threat of climate change due to geographical isolation. As an alpine species, if climate warming shifts the temperatures in these habitats outside the species' thermal tolerance range, extinction of populations may occur if adults are unable to migrate to new habitats (Parmesan, 2006).

Two primary research questions are addressed in this study. First, how does a changing temperature regime affect larval development and adult emergence in *P. smintheus*? Second, how do these temperature shifts indirectly influence reproduction in the adult population? To address these questions of direct and indirect temperature effects on larval development and adult reproductive success, we propose a novel mathematical model to predict temperature-dependent transition probability through larval instars. This larval development model is expressed as a multi-outcome discrete-time Markov process, where the transitional success probability is explicitly a function of daytime temperature. From this model, we predict adult emergence as a function of the temperature timeseries experienced by the larvae, and as such consider the indirect effects of temperature on reproductive success via the changes in emergence. The reproductive success model is expressed as a system of differential equations that track adult populations of males, unmated and mated females, and the resultant eggs produced. We parameterize our larval development and reproductive success models using experimental data for *P. smintheus* and we find that the larval development model produces adult emergence curves statistically indistinguishable from mark recapture data. When we use the adult emergence functions as input to the reproductive success model, we find that increasing temperatures increased reproductive success via increased successful emergence, and that a temperature-dependent reproductive success threshold for population growth appears, indicating a temperature-driven Allee effect at low population densities.

2 Methods

2.1 Larval development model

To address the question of the direct effect of temperature on the larval development process, we constructed a mechanistic model of larval development in which progress to adulthood is temperature-dependent. This model allows us to predict adult emergence in a summer given that year's temperature profile as input. We present a multi-outcome discrete-time pure-birth Markov process with mortality to model the temperature-dependent transition and mortality of an insect proceeding through larval instars.

Let the probability of a larva's presence in the ith instar on the nth timestep be denoted p^i_n. The probability of death on the nth timestep in the ith instar is d_i (an n-independent constant) and the temperature-dependent transition probability is $\mu_i(T_n)$, where T_n is the temperature on the nth timestep. A schematic of the model is presented in Figure 1. The four outcomes of each timestep with their associated probabilities are as follows: no transition and survival with probability $(1-\mu_i(T_n))(1-d_i)$, no transition and mortality with probability $(1-\mu_i(T_n))d_i$, transition and survival with probability $\mu_i(T_n)(1-d_{i+1})$, and transition and mortality with probability $\mu_i(T_n)d_{i+1}$. The probability of a larva's presence in a given class in a given timestep is then governed by the following set of master equations:

$$p^1_{n+1} = [(1-\mu_1(T_n))(1-d_1)]\, p^1_n \tag{1}$$

$$p^2_{n+1} = [(1-\mu_2(T_n))(1-d_2)]\, p^2_n + [\mu_1(T)(1-d_2)]\, p^1_n \tag{2}$$

$$\vdots$$

$$\underbrace{p^i_{n+1}}_{\substack{\text{probability larva is in}\\ i\text{th instar on } n\text{th timestep}}} = \underbrace{[(1-\mu_i(T_n))(1-d_i)]\, p^i_n}_{\substack{\text{probability larva was in}\\ i\text{th instar on } (n-1)\text{th timestep}\\ \text{and survived without transition}}} + \underbrace{[\mu_{i-1}(T)(1-d_i)]\, p^{i-1}_n}_{\substack{\text{probability larva was in}\\ (i-1)\text{th instar on } (n-1)\text{th timestep}\\ \text{and successfully transitioned}}} \tag{3}$$

$$\vdots$$

$$p^r_{n+1} = p^r_n + \mu_{r-1}(T_n)\, p^{r-1}_n. \tag{4}$$

where the rth class in which individuals accumulate is adulthood. We considered transitional probabilities to be linear functions of temperature

$$\mu_i(T_n) = \begin{cases} a_i(T_n - T_0), & T_n \geq T_0 \\ 0, & T_n < T_0 \end{cases}$$

where a_i is a constant of proportionality estimated from transitional success data, and T_0 is the species-specific thermal lower bound at which development can occur. We used initial conditions $p^1_{n_0} = 1$, $p^2_{n_0} = \cdots = p^r_{n_0} = 0$, so that all individuals begin in the first instar at some hatching time n_0.

The probability of emergence as an adult on the nth day, denoted as ϵ_n, was found by first successively solving the above system of equations numerically to obtain p^{r-1}_n, the probability of a larva's presence in the final larval instar on the nth day. Then the emergence probability is given by

$$\epsilon_n = \mu_{r-1}(T_{n-1})p^{r-1}_{n-1}, \tag{5}$$

where the probability of the adult emergence is the probability of both successful transition to adulthood and the presence of the larva in the previous instar. We used this adult emergence function to examine the direct effects of temperature on larval development, and present model predictions versus observed adult emergence in *P. smintheus* to demonstrate the model's utility in Section 3.1. Parameterizing the model with estimates for *P. smintheus*, we used temperature data for 2001 and $2003-2009$ as input and compared observed versus predicted emergence (5) with statistical tests presented in Section 2.5. Thus, using a series of difference equations modelling the temperature-dependent life history events of a larva, we predicted adult emergence based on the temperatures experienced by larvae. This adult emergence function was then incorporated into a model of reproductive success in adults, as we discuss presently.

We interpolated the adult emergence distribution ϵ_n to obtain an emergence rate $\epsilon(t)$, which we used as input in the model of Section 2.2 which examines the dynamics of the reproducing adult population. We quantified how adult emergence changed with temperature by two measures: total adult emergence and standard deviation of the emergence curve. The total emergence was calculated by $\epsilon_T \equiv \int_{t_i}^{t_f} \epsilon(t)dt$, and represents the proportion of the population which successfully emerged to adulthood in the course of the season. The standard deviation σ is a measure of the width of the emergence function and was calculated by

$$\sigma = \sqrt{\int_{t_i}^{t_f} k^2\tilde{\epsilon}(k)dk - \left(\int_{t_i}^{t_f} k\tilde{\epsilon}(k)dk\right)^2},$$

where $\tilde{\epsilon}(k) = \epsilon(k)/\epsilon_T$ must be used since $\epsilon_T < 1$ in a system with larval mortality, requiring normalization to produce a probability distribution. These results are presented in Section 3.1.

In summary, by quantifying how shifting temperatures influence adult emergence, we linked environmental effects on larval developmental rates to a population-level quantity relevant to reproductive success, connecting two disparate parts of the insect's life cycle. The adult reproductive success model is now presented.

2.2 Reproductive success model

Temperature may affect the population dynamics of a species via multiple mechanisms, including directly through larval development rates and indirectly through the effect these rates have on subsequent adult mating success by way of the emergence distribution. We quantified this indirect effect of temperature with an adult reproductive success model. In joining the two models together, we considered population growth over the course of a full generation, from the initial number of eggs at the beginning of the season, to the final number of eggs at the end of the season.

A reproductive success model for a semelparous insect species with monandrous females was constructed based on Calabrese et al (2008). Let M, U, R, and E be the number of adult males, unmated adult females, reproducing adult females, and eggs, respectively. A dynamical model which tracks these quantities over time throughout a single season is presented here as a system of non-linear coupled ordinary differential equations (ODEs).

In the year τ,

$$
\begin{aligned}
\underbrace{\frac{dM_\tau}{dt}}_{\substack{\text{rate of change}\\ \text{in \# males}}} &= \underbrace{\theta_M E_{\tau-1}(t_f)\epsilon(t)}_{\text{emergence of males}} - \underbrace{\gamma_M M_\tau}_{\text{male mortality}} \\
\underbrace{\frac{dU_\tau}{dt}}_{\substack{\text{rate of change}\\ \text{in \# unmated females}}} &= \underbrace{\theta_F E_{\tau-1}(t_f)\epsilon(t)}_{\substack{\text{emergence of}\\ \text{unmated females}}} - \underbrace{\gamma_F U_\tau}_{\substack{\text{unmated female}\\ \text{mortality}}} - \underbrace{cM_\tau U_\tau}_{\text{mating success}} \\
\underbrace{\frac{dR_\tau}{dt}}_{\substack{\text{rate of change}\\ \text{in \# mated females}}} &= \underbrace{cM_\tau U_\tau}_{\text{mating success}} - \underbrace{\gamma_F R_\tau}_{\substack{\text{mated female}\\ \text{mortality}}} \\
\underbrace{\frac{dE_\tau}{dt}}_{\substack{\text{rate of change}\\ \text{in \# eggs}}} &= \underbrace{\beta R_\tau}_{\text{egg production}} ,
\end{aligned}
\tag{6}
$$

where θ_M and θ_F are proportions of eggs which are male and female, γ_M and γ_F are constant male and female per-day death rates, c is a constant per-day mating rate, and β is a fecundity rate (average number of eggs produced per mated female per day). The adult emergence rate $\epsilon(t)$ is continuous and integrates to give the total proportion of the population which successfully emerges in the season, so $\epsilon_T < 1$ unless no larval mortality occurs. Note that $\epsilon(t) \geq 0$ for all t.

The evolution of the model falls in the time domain $[t_i, t_f]$, where t_i is the snowmelt date at which egg hatching occurs, and t_f is the season end date, based on field observations of when adults have stopped flying. The initial conditions for the above model are $M_\tau(t_i) = U_\tau(t_i) = R_\tau(t_i) = E_\tau(t_i) = 0$, where t_i corresponds to the discrete n_0 used to generate the adult emergence function $\epsilon(t)$. Successive years $\tau - 1$ and τ are connected by the number of eggs produced in year $\tau - 1$, or $E_{\tau-1}(t_f)$. This acts as input to the male and unmated female equations of the adult reproductive success model in year τ, as it represents the egg populations from which these populations are generated. The in-season population dynamics of the model thus produce a number of eggs which act as input to the male and unmated female populations in the next year. We ignored over-winter mortality in the eggs. This type of model, with continuous-time dynamics for part of the year (the emergence and breeding period, in this case) with repeated discrete changes (linking eggs produced in year $\tau - 1$ with the input of eggs in year τ) has recently been classified as a *semi-discrete model* (Mailleret and Lemesle, 2009).

We used this model to explore the indirect effects of temperature on adult reproductive success. That is, as temperature shifts influence larval development, so these changes to larval development impact adult reproduction. To quantify the effect of temperature on adult reproductive success, we used the coupled larval development and adult reproduction models to explore how changing temperatures as experienced by larvae would affect adult population dynamics through the emergence function. Reproductive success in a year was defined to be a net increase in eggs from year $\tau - 1$ to year τ, or $E_{\tau-1} < E_\tau$. The reproductive success threshold $E_\tau/E_{\tau-1} = 1$ represents the point at which the population replaces itself from year to year. By choosing some initial input of eggs and a temperature profile for a year, we computed adult emergence using the larval development model, input it in (6), and numerically solved the system of ODEs to predict the number of eggs at the end of the season, $E_{\tau+1} = E_\tau(t_f)$. In this way, the models act as a mapping of initial to final number of eggs in a year, and allowed us to examine how changing temperatures impacted this mapping. We studied how the reproductive success threshold depends on temperature through numerical simulations of both models with changing temperature inputs. These results are presented in Section 3.2.

In summary, by constructing a mechanistic temperature-dependent adult emergence function (5), we connected larval development to subsequent reproductive success, and developed tools to determine how temperature changes corresponding to climatic shifts might impact a species such as *P. smintheus* both directly at a physiological level and later through emergence effects on adult population dynamics. We identified measures of change to emergence and change to adult reproductive success based on spring and summer temperatures.

2.3 Experiments and datasets

The effect of temperature on phenology is a poorly understood aspect of *P. smintheus* life history. To parameterize a model of larval development with temperature-dependent transition probabilities, we thus needed to determine a plausible biological range of such transition probabilities experimentally. To this end, we conducted an experiment to record transitional success and failure, as well as mortality, in *P. smintheus* larvae under a range of temperatures.

The data used for parameterization of the larval development model was collected in a growth experiment of *P. smintheus* larvae collected from field sites at Lusk and Jumpingpound Ridges ($51°57'$ N, $114°54'$ W), both in Kananaskis, Alberta, Canada. The larvae were reared with sufficient food in one of three growth chambers: the first mimicked historical ambient field temperatures in the range of $10 - 15°$ C, the second elevated this temperature profile by $2°$ C, and the third lowered it by $2°$ C. Mortality and transitional success of all larvae were recorded daily. The results of this experiment and a more detailed discussion of the experimental procedure are documented in Matter et al (2011).

The predicted adult emergence function was validated using mark-recapture data collected for *P. smintheus* adults in Kananaskis, Alberta, over a period of eight years (Roland et al, 2000; Matter and Roland, 2002; Matter et al, 2003, 2004; Roland and Matter, 2007; Matter et al, 2009). Adults were marked at first capture in a meadow, and each meadow was sampled on multiple days throughout the season. To obtain the observed probability of emergence from the mark-recapture data, we summed the number of first captures in a meadow between two successive sampling days and divided this sum over the total number of adults captured in the meadow throughout the season. This is the probability of adult emergence between the successive sampling days which corresponds to the sum of the emergence probability between those two days as predicted by the larval development model. Dispersal events (to other fields blocked by forest boundaries), which would influence observed emergence between sampling days, were rare, with at most 3.8% of the adult population observed to migrate to a spatially unconnected region in a given summer (Matter et al, 2004).

In addition to the usual utility of these datasets for model parameterization and validation, the differing character of the two datasets provided a test of the consistency of the biological model, as growth chamber data was used to parameterize coefficients while predictions were validated against emergence data.

2.4 Parameter and error estimation

We parameterized the larval development model using experimental growth data in which for each day's temperature T_n there exists multinomial transitional success/failure and mortality data.

The experimental growth data provided, for each larva in the experimental trials, a precise trajectory through the developmental process. This trajectory was comprised of a list of outcomes for each experimental day n associated with temperature T_n on that day. The possible outcomes are survival without transition, mortality without transition, transition and survival, and transition and mortality. From the larval development model, each such developmental trajectory corresponded to a probability consisting of the product of component probabilities for each outcome on each day of the larva's development. For instance, for a fourth instar larva in a given four day period with temperatures $\mathbf{T} = [T_1, T_2, T_3, T_4]$, where the larva successfully transitioned on the third day, that part of the trajectory's probability would appear as

$$(1-\mu_4(T_1))(1-d_4)(1-\mu_4(T_2))(1-d_4)\mu_4(T_3)(1-d_5)(1-\mu_5(T_4))(1-d_5).$$

This probability indicates that the larva survived without transitioning for two days in the fourth instar, transitioned successfully on the third day, and survived the fourth day without transitioning in the fifth instar. Recall that $\mu_i(T_n) = a_i(T_n - T_0)$, so the parameters to be estimated from data were a_i and d_i for $i = 1, \ldots, 6$.

We determined maximum likelihood estimates for each parameter in the following way. For each larva, the full probability of its observed trajectory was computed as in the example above in terms of the a_i and d_i terms. As each larval trajectory was independent, these probabilities were then multiplied together into a likelihood function corresponding to the probability that our precise experimental dataset was observed. The resulting likelihood function depended on the parameters a_i and d_i in a separable manner, so that each could be maximized independently of the others.

Since we did not model mortality as temperature-dependent, those components of the likelihood function were not time-dependent. This resulted in an analytic form of the maximum likelihood estimates for d_i expressible as:

$$\hat{d}_i = \frac{x_a^i}{x_a^i + x_b^i}, \tag{7}$$

where x_a^i denotes the total number of mortality events in the instar among all larvae and x_b^i denotes the total number of survival events in the instar. As per the above single larva example, x_a^i would be the exponent on d_i and x_b would be the exponent on $(1 - d_i)$ in the likelihood function. As no strong change in mortality occurred across the instars, we used a single mortality probability estimate $\hat{d}$ to be the mean of the instar estimates. Because $\hat{d}$ is a binomial proportion of successes, we used an adjusted Wald 95% confidence interval for this parameter.

Given the temperature-dependence of the likelihood functions associated with the transitional success probabilities in each instar, we maximized these functions numerically. Because $\mu_i(T_n)$ is a two-parameter function, we fixed T_0 with a biologically reasonable value (see Table 1) and obtained a maximum likelihood estimate for the slopes a_i. For consistency, it was necessary to bootstrap the transition data due to a larger sample size in the low temperature treatment. Random samples of the same size were selected at each temperature and the estimate taken for a_i was the mean of maximum likelihood estimates over one thousand such random selections. The 95% confidence intervals for a_i were computed directly from the interval in which 95% of bootstrapped estimates fell. These confidence intervals, as well as those for mortality d_i, gave parameter errors which were summed in quadrature to obtain the error which propagates through the larval development model to adult emergence (Taylor, 1997).

In the reproductive success model, we used values estimated by Calabrese et al (2008) for mating rate c, and proportions of males and females θ_M and θ_F. We estimated the fecundity rate β and female mortality rate γ_F from fecundity experiments documented in Matter et al (2009), and a confidence interval for β was calculated assuming a normal distribution for the fecundity rate (Table 1). Male mortality rate was estimated to be slightly lower than female mortality rate, as males have been observed in the field to live for approximately two weeks.

The transition and mortality parameters for the larval development model were estimated from experimental growth data, while the demographic parameters for the adult reproductive success model were primarily taken from the literature (sex ratios, mating success rate, and adult mortality), and reproductive rates were estimated from fecundity experiments (Table 1).

2.5 Model validation and statistical analyses

We validated the model with statistical tests to compare model performance against the observed adult emergence distributions discussed in Section 2.3. The validation ensured that the larval development model gave biologically reasonable results prior to its substitution into the reproductive success model.

Observed versus predicted emergence on a given day were compared using both a Wilcoxon signed-rank test and linear regression of observed emergence on predicted emergence. Because sampling did not occur every day, the model predictions were aggregated to sampling days in this analysis, as described in Section 2.3. The null hypothesis states that observed and predicted emergence on a given day are the same, while the alternative hypothesis states that they differ. The linear regression analysis evaluates model validity by regressing observations on predicted values. The null hypothesis states that the slope and x-intercept of the regression line are 1 and 0, respectively, while the alternative hypothesis states that these values are not 1 and 0. To find evidence for the observed and predicted emergence distributions being statistically indistinguishable, a non-rejected null hypothesis was desired in both tests.

3 Results

All parameter values used are summarized in Table 1, which are computed using the techniques presented in Section 2.4.

3.1 Larval development model

Under this parameterization, a plot of predicted versus observed emergence in 2008 is presented as an example in Figure 2. Because field data exists for emergence distribution but not total fraction of successful emergence (that is, no field larval mortality data exists), we normalized field data by the model's predicted larval mortality so that a meaningful comparison of the observed and predicted emergence can be made. The statistical results of the validation are summarized in Table 2: using the Wilcoxon signed-rank test, no significant difference was detected between predicted and observed emergence in all years, save for 2005 when too few sampling days precluded the use of the test. The linear regression of observed on predicted emergence probabilities detected no significant difference between the predicted and observed emergences in any year save 2009. We will address in the discussion a potential mechanism for the discrepancy in the two tests in 2009.

The effect of changing daytime temperatures on predicted adult emergence rate is also considered. Increases in temperature are observed to increase the emergence rate (shown in Figure 3 with 2008 temperature data as input), and in Figure 4 we see more specifically that the increase in temperature increases both the total proportion of the population which successfully emerges as adults over the course of the season, ϵ_T (Figure 4a), and the standard deviation of the emergence curve, σ (Figure 4b).

3.2 Reproductive success model

As discussed in Section 2.2, the reproductive success model acts as a mapping between the initial number of eggs E_τ in a given year τ and the initial number of eggs in the subsequent year, $E_{\tau+1}$. The cobweb diagram of Figure 5a indicates the non-linear effect of varying the initial number of eggs in a year on the number of eggs present in successive years. The curves show the mapping of E_τ to $E_{\tau+1}$ in 2006 through 2008, which differ since the temperature time series were different in each year. The solid 45° line represents the reproductive success threshold within a year. That is, if a given year's curve lies above the reproductive success threshold for that year's initial egg count, then the population will increase between that year and the subsequent year. Likewise, if the curve lies below the reproductive success threshold for that year's initial number of eggs, then the population decays. Since the number of eggs in the next year depends on the number of eggs this year, the intersection of each curve with the reproductive success threshold indicates the initial number of eggs at which the population exactly replaces itself within that year, where $E_\tau = E_{\tau+1}$. We refer to the initial number of eggs at which this intersection occurs as the persistence point.

In the scenario denoted by the solid lines, initial egg densities in 2006 are low, $E_{2006} = 6000$ eggs, and the predicted number of eggs increases slightly in $2006 - 2007$ before decreasing in both $2007 - 2008$ and $2008 - 2009$ (see the solid line in Figure 5b for the associated timeseries). In the scenario denoted by the dashed lines, initial egg densities in 2006 are twice as high, $E_{2006} = 12000$ eggs, and the predicted number of eggs increases between $2006 - 2007$ and $2007 - 2008$, before decreasing in $2008 - 2009$ (dashed line in Figure 5b). So, by doubling the initial number of eggs, the predicted number of eggs increases in $2007 - 2008$ rather than decreasing, and after a three year iteration, the predicted number of eggs for 2009 is more than twice as large as that predicted from an initial count in 2006 half as large.

The persistence point is plotted as a function of daytime temperature shift in Figure 6, which shows that the number of eggs required to replace the population decreases with increasing temperature shifts. In 2006, in the absence of temperature shifts, the persistence point occurs at $E_{2006} = 1247$ eggs while in 2007, it occurs at $E_{2007} = 13350$ eggs. In 2008, the persistence point is not attained without temperature shifts, and an increase of 1.5° C in daytime temperature is required to numerically find the persistence point. Figure 6 also demonstrates the existence of a temperature-driven Allee effect: for a given temperature timeseries with no temperature shift, the persistence point occurs at some initial number of eggs, which indicates the initial number of eggs required to maintain the population that year. However, as the temperature timeseries is cooled, this initial number of eggs below which the population cannot persist increases, becoming infinite at finite temperature shifts. This indicates that the population cannot possibly replace itself and demonstrates that lower temperatures aggravate the Allee effect in these cooler years.

4 Discussion

4.1 Overview

In this study, advances were made in understanding the effects of temperature on the phenology of the alpine butterfly *P. smintheus*. Using a combination of experimental and modelling approaches, the effect of increasing temperatures was demonstrated to decrease larval developmental times, prompt earlier and higher adult emergence, increasing population growth. Our goal was to link environmental conditions in the larval stages to subsequent adult demography, and highlight the indirect effects that temperature can have on reproductive success. We approached this problem by constructing a mechanistic model to predict larval development and adult emergence. With this mechanistic framework validated by mark-recapture field data, we incorporated the larval development model into a model tracking adult reproductive interactions.

Through this model, we identified positive effects of increased temperature on population persistence through the mitigation of an Allee effect otherwise present at low population densities. Our experimental and modelling results suggest that *P. smintheus* is not presently near its thermal maximum and that rising spring and summer temperatures may actually increase larval survival and subsequent adult reproductive success. From a broader perspective, the modelling framework that we have proposed can link multiple components of a species' life history and address effects of temperature on phenology and population growth over the course of years within different scenarios of climatic change.

4.2 Model and data limitations

The purpose of incorporating the larval development model into the reproductive success model was to map the initial egg count within a year to the final egg count, and in that way establish a link between temperatures experienced by larvae and population growth. However, this approach was burdened by the large number of parameters that cannot be measured exactly, leading to error propagation through the model. Additionally, the growth experiments that we conducted represented the first attempt to understand effects of temperature on larval phenology in *P. smintheus.* Given that ours was the first experiment in this area, the deficit of data is not surprising, nor is the extent of the confidence intervals on parameter estimates. This parameter uncertainty impeded quantitative predictions of *P. smintheus* population dynamics from year to year. The larval mortality parameter d was the most problematic to the model system as it contributed the most error to the reproductive model output (egg production in a given year). Furthermore, the reproductive success model suggested that larval mortality may be overestimated in the current model: we correctly predicted population increases in 2006 and 2007, and a population decrease in 2009, but erroneously predicted population decreases in both 2005 and 2008 under the present parameterization. Such unexpected decreases in the model predictions could also be due to an underestimated fecundity rate β, which had the second highest contribution to error in egg production. It is evident that quantitative prediction requires further experimental work to narrow the confidence intervals on the parameter values. A quantitative model for reproductive success would also require a better understanding of overwinter survival of *P. smintheus* eggs, which may also be regulated by temperature and precipitation. Overwinter mortality was not considered in this framework, a simplification which impedes quantitative prediction of population dynamics. However, this offers still further evidence that d was overestimated or β was underestimated: since the model predicted two false population decreases and no false population increases, this effect would only be exaggerated by overwinter mortality.

In our mechanistic larval development model, we used a simple temperature-dependent transition probability function, a linear increase in transition probability with temperature. This choice was motivated by its simplicity, the experimentally unknown nature of the effects of temperature on *P. smintheus* larval development, and an experimental temperature range well within the field temperature range observed for *P. smintheus*. For such a temperature range, non-linear developmental effects would not be anticipated. Future experimental work would involve expanding the temperature range toward thermal extrema and fitting the data to potentially non-monotonic transitional probability functions, to reflect current understanding of insect development at high and low temperatures (Taylor, 1981).

Despite some simplifications and uncertainty in parameter estimates, the larval development model captured observed emergence to the point of statistical indistinguishability, and the adult reproductive success model produced interesting dynamical results with important ecological implications, as we discuss in the next two sections.

4.3 Larval development model

The larval development model predicted an emergence temporally synchronous with the observed emergence in all years for which temperature data was available, and was statistically indistinguishable from observations. While the confidence intervals of the estimates were large (Table 1), as discussed in the previous section, the estimates demonstrated a strict decrease as instars increased, indicating that an individual in the third instar at a given temperature has a larger transitional probability than a member of its cohort in the sixth instar. This offers some evidence that the parameter estimates were biologically reasonable, as energy requirements may be higher in later instars and prompt longer development times.

The estimates for a_i were further influenced by the fixed value of T_0, the thermal lower bound for development, since this parameter was fixed prior to either maximum likelihood estimation or bootstrapping for a_i. The experimental data offered little insight into what such a parameter value might be, as the experimental temperature range was too high to prompt a cessation in development for any individual. A review of the literature prompted the fixed $T_0 = 5^\circ$ C, as it is seen in multiple butterfly species (Hill et al, 1999; Taylor, 1981) as an approximate lower developmental threshold for larvae. Model robustness to a varying T_0 was tested by varying T_0 and estimating the slopes $\hat{a}_i$ from development data. For each temperature in the range $T_0 = 3 - 6^\circ$C, the resulting estimates for $\hat{a}_3$ and $\hat{a}_6$ fell within the confidence intervals for estimates at each other temperature in this range. The same held for $\hat{a}_5$ for $T_0 = 3 - 5^\circ$, and for $\hat{a}_4$ for $T_0 = 4 - 5^\circ$. We concluded that the model demonstrated some robustness to variations in T_0.

A comparison of predicted versus observed emergence in *P. smintheus* adults lent some support to the model's validity. The Wilcoxon signed-rank test (Table 2) did not reject the null hypothesis that observed and predicted emergence distributions were the same (excepting 2005, when an insufficient number of sampling days precluded the use of the test). A linear regression of observed on predicted emergence probabilities (Table 2), rejected this same null hypothesis in 2009 only. This rejection may have been due to model failure, but may also have been due to the large amount of variability in the data, which can cause Type I errors in linear regression analysis (Haefner, 2005).

The model was also found to be robust to changes in start date t_i, due to very low temperatures in the range of hatching dates used. Model robustness to variation in start date was examined over the range of dates from April 15th to June 3rd. This range of start dates was chosen as hatching in *P. smintheus* is triggered by snowmelt, so sufficiently high temperatures were required prior to the calendar day on which the model simulations were to begin. Given that transitional probabilities were zero at temperatures lower than 5°C, we found that the adult emergence distribution changed very little in shape or range given simulated hatching dates from April 15th to June 3rd, due to low temperatures within these time periods. Care was still taken when fixing simulated hatch dates, however, as the constant daily mortality probability used in the model caused lower overall adult emergence in simulations where hatching occurred earlier (as individuals trapped in first instar by low temperatures fell prey to mortality).

Understanding the developmental behaviour of *P. smintheus* near the thresholds of its developmental temperature range may be important in the context of climate change, which may cause warming as well as increased variability in temperatures. If warm years prompt early and brief emergence periods, it may have a profound effect on population and community dynamics. The early emergence from faster larval development (as demonstrated both experimentally and through modelling) may confer both advantages and disadvantages to a population. Experimental results (not shown here) suggested that mortality was lower in faster developing larvae, so that more larvae successfully reached adulthood. Growth experiments in *Proclossiana eunomia* indicate death rates in adults increase in time from first emergence, possibly caused by higher fitness in early emerging individuals or increasing competition for limited resources (Schtickzelle et al, 2002), though it is unknown whether such a pattern is present in *P. smintheus*. The present larval development model treated individuals as identical, so individual effects cannot be captured.

Temperature-driven effects on adult emergence must also be studied at a community level. *P. smintheus* emergence synchrony with host plants, both at larval and adult stages, is critical to population survival (Fred and Brommer, 2010; Matter et al, 2009). Warming temperatures may destabilise the synchrony of these interacting species or even force species out of a previously shared habitat. The effects of temperature on interacting species is thus an important subsequent step to this research.

The adaptation of the model to consider protandry and sex-specific larval development constitutes an additional avenue of future research. Protandry has been observed in *P. smintheus* adult populations, with earlier initial emergence of males than females (Calabrese et al, 2008). The current model framework permits protandrous species modelling, given sex-specific development data; separate parameterizations for male and female larvae would allow two distinct adult emergence distributions. Protandry was not considered in the present study as male and female *P. smintheus* are physically indistinguishable in their larval form. That is, while individuals surviving to adulthood may be sexed *a posteriori*, no information can be determined from individuals dying prior to adulthood. While it is possible to genetically determine sex after death in larvae, such analysis was beyond the scope of the present study.

Motivation for our experimental and modelling studies were drawn from the considerable ecological implications to a population from temperature-induced phenological changes. Our study offered evidence for temperature as a driving factor in phenological changes to *P. smintheus* larvae and emerging adults. Our larval development model was then extended into an adult reproductive success model to address the resultant effects of these phenological changes on adult population dynamics. Despite some uncertainties in the parameter values, the model captured well the temporal range of the observed emergence and also captured the shape of the emergence curve (Figure 2). Two statistical tests found the predicted emergence to be indistinguishable from field data. We thus concluded that our model captured the effect of temperature on adult emergence in a reasonable manner, and our predicted emergence was suitable for use in the examination of the indirect effects of changing temperature on adult reproductive success.

4.4 Reproductive success model

Increasing temperatures increased both total adult emergence and the standard deviation of the emergence function. This result suggests a competing effect in increasing temperatures from a reproductive perspective. A larger proportion of adults emerging suggests a positive effect on mating-finding and thus reproductive success (unless such successes are overshadowed by increased resource competition). However, increases in standard deviation of emerging populations is indicative of increased asynchrony. From a biological standpoint, a decreasing standard deviation means a briefer period of highly synchronized emergence among individuals in a population (Calabrese and Fagan, 2004). Iwasa and Levin (1995) and Post et al (2001) proposed that asynchrony (higher standard deviations in emergence) increases in cases of environmental perturbation, though their results are not specific to insects. Further, Yurk and Powell (2009) suggested that developmental synchrony is temperature-dependent and that insects lose synchrony outside a narrow range of temperatures. Thus it may be reasonable to expect greater asynchrony in populations faced with warming temperatures, so an increasing standard deviation in adult emergence at higher temperatures in the present model may be biologically realistic. This argument may be sensitive to the functional form of temperature-dependent larval development. While Yurk and Powell (2009) suggested a narrow range of temperatures at which emergence synchrony occurs, we observe a strictly increasing relationship of standard deviation with temperature. That is, there is no cooler temperature regime, according to this model, where synchronous emergence will shift towards asynchronous emergence. The increasing relationship of temperature and standard deviation is illustrated in a 6°C range in Figure 4b. However, given that we predicted an increase in reproductive success with temperature (Figure 6), we concluded that the increased proportion of adults that emerge is a stronger effect on reproductive success than when the adults emerge. Inspection of Figure 3 indicates how total emergence remains a stronger effect: the increased standard deviation appears to result from the addition of tails onto the emergence distribution at higher temperatures. The addition of such a tail constitutes the addition of individuals into the population, and thus cannot adversely impact reproductive success. This quantitative measure of thermal effects on adult emergence provided the first insight into how past environmental experiences play out in adult population dynamics in *P. smintheus*.

The current model presents what may be a valid framework for studying multi-year temperature-forced reproductive success in *P. smintheus*, if error in the system can be controlled. The reproductive success model allowed iteration from year-to-year by the presence of some initial number of eggs E_τ, taken in the present study directly from the previous year's production $E_{\tau-1}$. The dynamics of our population model reveal the presence of a demographic Allee effect aggravated by low temperatures (Figure 6). Such an Allee effect could potentially be disastrous for *P. smintheus* population persistence, as severe population crashes have been observed in the past (Matter and Roland, 2010). The reproductive success model presented here demonstrated this Allee effect from a mechanistic, biologically-motivated model. Previous models for butterfly population dynamics have considered phenomenological emergence functions such as stretched Beta distributions (Calabrese and Fagan, 2004) and Gamma distributions (Calabrese et al, 2008), but these were not chosen based on a biological mechanism, unlike the temperature-dependent emergence function developed in the present study. Our mechanistic modelling approach and associated demographic Allee effect show similarities to those observed in the models presented in Veit and Lewis (1996), McCarthy (1997), Drake (2004), Molnár et al (2008), Jerde et al (2009), and Wittmann et al (2011). Only Wittmann et al (2011), however, identified temperature explicitly as a potential driver of reproductive success, suggesting that there remain many open pathways toward modelling temperature-dependent reproductive success and the potential for Allee effects.

The reproductive success model as presented is a simple model in most respects, with constant adult mortality rates, coupling rate, and fecundity rate. Calabrese et al (2008) presented multiple functional forms for coupling rate in *P. smintheus*, finding that inverse male density fit better to data than a constant rate, so a similar analysis to that presented here with a more complicated coupling function is a viable area for further research. Fecundity may also be more complicated than a constant rate would indicate. In fact, temperature influences fecundity in *P. smintheus* as egg production by mated females is partially dependent on resources available to larvae (Matter et al, 2006). Effects of temperature on larval food source and adult fecundity represent imperfectly understood areas on how thermally-affected food sources may indirectly influence population dynamics. Temperature may also influence fecundity directly: increased temperatures have been linked to increased fecundity rates in butterflies *Pararge aegeria* (Gibbs et al, 2010) and *Bicyclus anynana* (Steigenga and Fischer, 2007). At present, direct effects of temperature on *P. smintheus* fecundity are unknown.

Should a more complicated temperature-dependent fecundity function be introduced into the adult reproductive success model, it would also introduce another non-autonomous element to the system. In the present model, only emergence rates depend on time, but if fecundity rate was modelled as temperature-dependent, it would also be implicitly time-dependent. If so, the temporal dependence of the emergence function could influence the adult dynamics via additional mechanisms. For instance, at present, an increase in temperature influences the reproductive success model through increasing total emergence and decreasing synchrony. However, increased temperatures in the larval developmental model also led to earlier emergence, an effect which is irrelevant in the adult reproductive model because there is no explicit time-dependence outside the emergence function itself. That is, if emergence shifts in time, it does not currently influence reproductive success. If fecundity were to be modelled as time-dependent, however, then these shifts in emergence time would begin to influence adult mating dynamics.

As mentioned previously, overwinter mortality is at present neglected in the model dynamics, a simplification which makes quantitative predictions about population dynamics difficult. Current research for *P. smintheus* suggests that climate is an important factor in overwinter egg survival, with higher mortality in drier winters, when there is little snow insulation to prevent freezing and desiccation (Matter et al, 2011). Further research is necessary to determine the magnitude of influence of spring and summer temperatures (affecting larval growth and adult reproductive success) compared to winter temperatures (affecting egg survival) on the persistence of the population.

5 Conclusions and future work

In this study, we advanced the previously limited understanding of temperature effects on *P. smintheus* populations, both through direct changes to larval and emerging adult phenology and through indirect effects on subsequent adult reproductive success. We constructed a general model framework which allowed the disparate elements of an insect's life history to interact and affect population growth.

Further work in this area would involve an extended growth experiment to study thermal effects nearer to larval thermal tolerances, which would allow parameterization of the model to a wider range of climatic scenarios. With this data we could also explore varied temperature-dependent transitional success functions for the larval development model. Subsequent experimental work would also narrow the confidence intervals on the parameter estimates and lead us to a quantitative model prediction of population dynamics from year to year, allowing for a better understanding of how climate change will affect the alpine meadow habitats that these butterflies inhabit.

We presented a model which addressed thermal effects on population dynamics from egg hatch to adult mortality, mapping the eggs from the beginning of the year to the eggs that replaced the population at the end. The missing link in this model from a life cycle perspective is the overwinter mortality of eggs, a subject that is presently being addressed (Matter et al, 2011). If we can incorporate a climatically-influenced overwinter mortality map into our model for *P. smintheus*, we will have a potentially powerful tool to predict effects of climate change on this butterfly species. From there, we can address the impacts that such changes to the population may have on its broader alpine habitat.

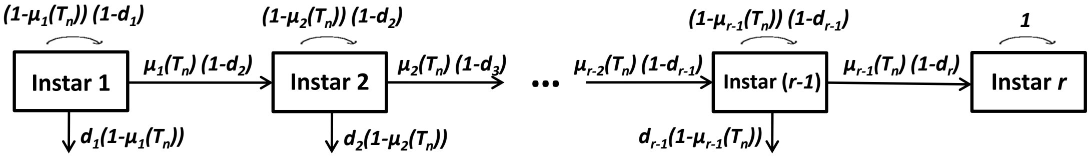

Fig. 1 Schematic representation of the r instar insect life history where $\mu_i(T_n)$ is the probability of leaving the ith class in the nth time step and d_i is the probability of mortality in the time step.

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Symbol	Units	Estimate	95% CI	Biol. Interpretation	Source
T_0	°C	5.0	–	Thermal lower bound at which larval development can occur.	(Hill et al, 1999; Taylor, 1981)
a_1	$°C^{-1}$	0.0123	$(0.0083, 0.0163)$	$a_i(T - T_0)$ is the daily transitional success probability out of the ith instar at temperature T.	Growth expt. data
a_2	$°C^{-1}$	0.0123	$(0.0083, 0.0163)$	See note for a_1.	Growth expt. data
a_3	$°C^{-1}$	0.0123	$(0.0083, 0.0163)$	See note for a_1.	Growth expt. data
a_4	$°C^{-1}$	0.0073	$(0.0062, 0.0084)$	See note for a_1.	Growth expt. data
a_5	$°C^{-1}$	0.0028	$(0.0023, 0.0033)$	See note for a_1.	Growth expt. data
a_6	$°C^{-1}$	0.0022	$(0.0019, 0.0026)$	See note for a_1.	Growth expt. data
d	dim'less	0.019	$(0.0151, 0.0299)$	Daily probability of mortality.	Growth expt. data
t_i	day	122	–	Numerical start date of (1-4), calendar day on which hatching is predicted to occur.	Temperature data
θ_M, θ_F	dim'less	0.5	–	Proportion of eggs which are male and female, respectively.	(Calabrese et al, 2008)
γ_M	$(\text{day})^{-1}$	0.0714	–	Death rate for male adults.	–
γ_F	$(\text{day})^{-1}$	0.1	–	Death rate for female adults.	(Matter et al, 2009), (Matter, pers. comm.)
c	$(\text{day})^{-1}$	0.061	–	Mating rate for adults.	(Calabrese et al, 2008)
β	$(\text{mated fem.} \cdot \text{day})^{-1}$	3.176	$(2.317, 4.035)$	Number of eggs produced per day per mated female.	(Matter, pers. comm.)
t_f	day	260	–	Numerical end date of (6), calendar day on which seasonal adult population is dead.	Mark recap. data

Table 1 Summary of parameters for adult emergence model (1)-(4) and reproductive success model (6).

Year	Num. observations	T+,T-	Tcrit	Conclusion	F	Fcrit	Conclusion
2001	7	7, 21	2	Do not reject H_0	2.57	8.43	Do not reject H_0
2003	6	7, 14	0	Do not reject H_0	1.48	10.6	Do not reject H_0
2004	7	6, 22	2	Do not reject H_0	1.97	8.43	Do not reject H_0
2005	5	−−	−−	Sample too small	0.45	16.0	Do not reject H_0
2006	11	23, 43	11	Do not reject H_0	1.19	5.71	Do not reject H_0
2007	20	72, 138	52	Do not reject H_0	3.80	4.56	Do not reject H_0
2008	18	69, 102	40	Do not reject H_0	3.75	4.69	Do not reject H_0
2009	17	57, 96	34	Do not reject H_0	9.03	5.26	Reject H_0

Table 2 Results of Wilcoxon signed-rank test on left and results of linear regression of observed on predicted emergence on the right. Predicted model emergence is not significantly different from observed emergence in all years for the Wilcoxon signed-rank test, and is significantly different in the linear regression only in 2009.

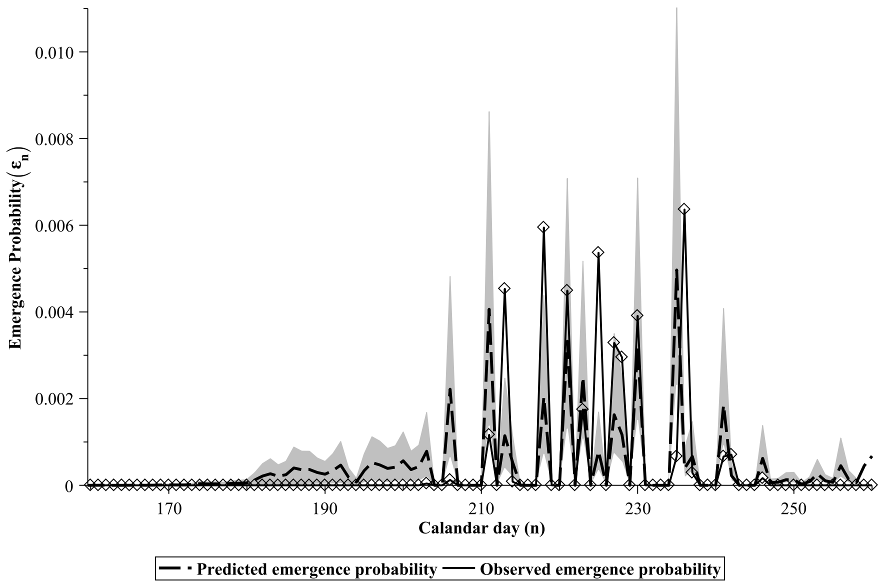

Fig. 2 Predicted versus observed emergence probability (ϵ_n) from 2008 temperature data. Predicted emergence uses parameter values from Table 1, and is denoted by the dashed curve with associated error shaded in grey, while observed emergence on sampling days is denoted by the solid curve with the diamond. Days on which the observed probability of emergence is zero are meant to indicate that no data was collected on those days. Predicted emergence with error is aggregated to sampling days.

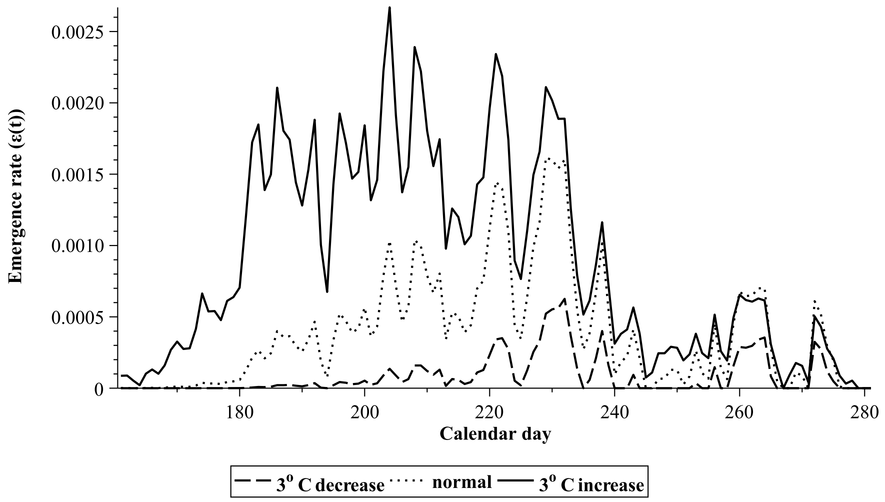

Fig. 3 Emergence probability ϵ_n per calendar day as predicted by the larval development model equations (1)-(4), using parameter values presented in Table 1. The predicted adult emergence curve for 2008 temperature data (dotted curve) increases when daytime temperatures are increased (solid curve) and decreases when daytime temperatures are decreased (dashed curve).

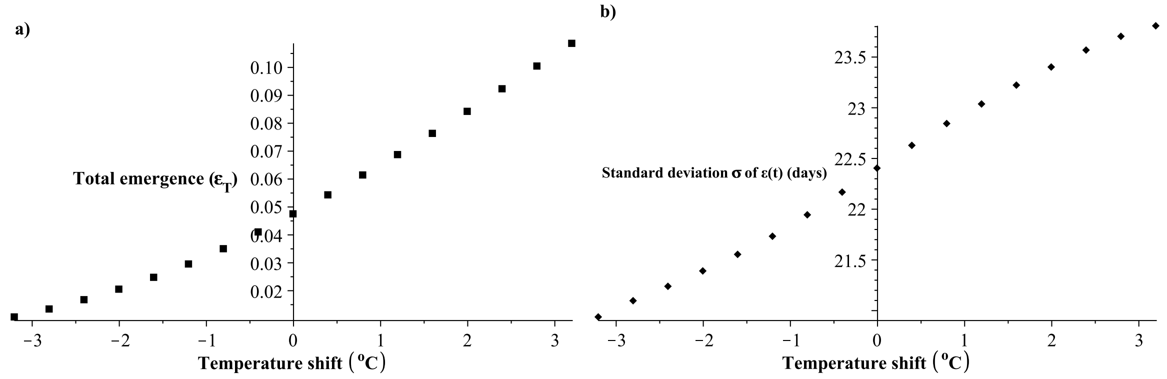

Fig. 4 a) Total emergence ϵ_T, or proportion of larvae which successfully emerge as adults and b) standard deviation σ of the emergence distribution $\epsilon(t)$ as functions of shifting daytime temperature. Increasing daytime temperatures increases both the total emergence and the standard deviation of the emergence curve. This simulation uses 2008 temperature data and the parameter values presented in Table 1.

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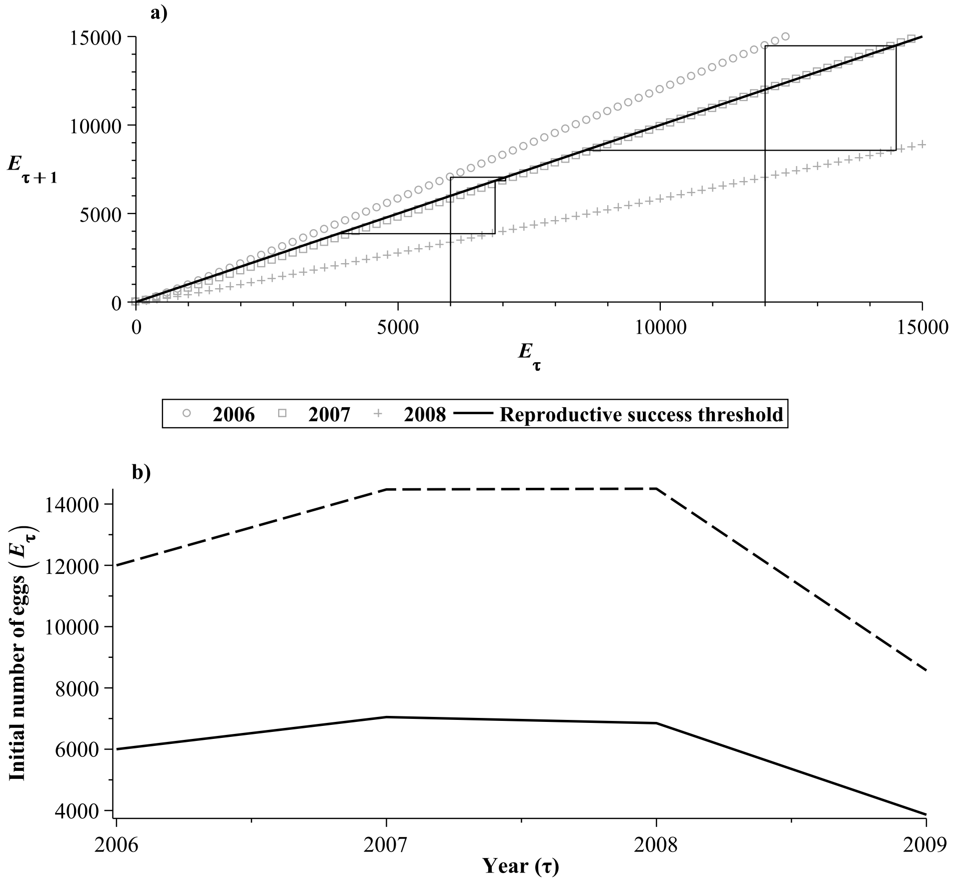

Fig. 5 a) Cobweb diagram illustrating nonlinear mappings of year-to-year egg counts for 2006, 2007, and 2008. The reproductive success model (6) maps initial egg densities (E_τ) to final egg densities ($E_{\tau+1}$) within a year which provide the basis for the next year's population growth. The curves here represent the predicted mappings based on temperature data in 2006, 2007, and 2008. Given low initial egg count $E_{2006} = 6000$ eggs (solid line), the model predicts $E_{2007} = 7048$ eggs, $E_{2008} = 6850$ eggs, and $E_{2009} = 3862$ eggs . When $E_{2006} = 12000$ eggs (dashed line), the predictions in successive years are $E_{2007} = 14476$, $E_{2008} = 14500$, and $E_{2009} = 8570$. b) Timeseries of predicted egg counts associated with the above cobweb diagram, where solid lines represent $E_{2006} = 6000$ eggs and dashed lines represent $E_{2006} = 12000$ eggs. The predicted numbers of eggs in 2009 are $E_{2009} = 3862$ and 8576, which differ by a factor greater than two.

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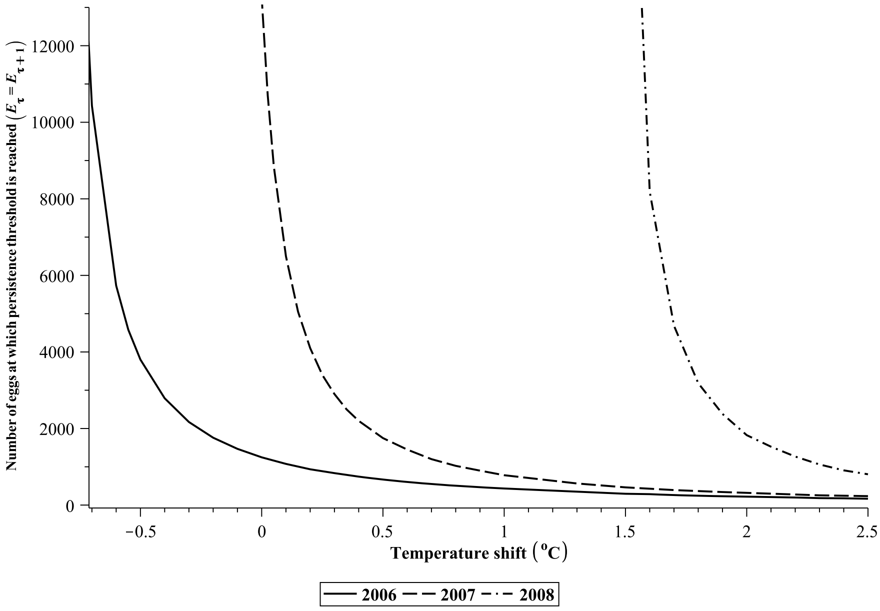

Fig. 6 Number of eggs at which the population replaces itself within a year ($E_\mathcal{T} = E_{\mathcal{T}+1}$) as a function of daytime temperature shifts. Increasing temperatures decrease the number of eggs ($E_\mathcal{T}$) required to replace the population for the following year. The simulations are based on temperature regimes recorded in 2006, 2007, and 2008, successively colder years, and parameter values presented in Table 1.

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