Journal of Insect Physiology 58 (2012) 634–647

Contents lists available at SciVerse ScienceDirect

Journal of Insect Physiology

journal homepage: www.elsevier.com/locate/jinsphys

Effects of temperature on development, survival and reproduction of insects: Experimental design, data analysis and modeling

Jacques Régnière [a,*], James Powell [b], Barbara Bentz [c], Vincent Nealis [d]

[a] Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre, P.O. Box 10380, Stn. Ste Foy, Quebec, QC, Canada G1V 4C7
[b] Department of Mathematics and Statistics, Utah State University, Logan, UT 84322-3900, United States
[c] Rocky Mountains Research Station, US Forest Service, 860 North 1200 East, Logan, UT 84321, United States
[d] Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, 506 West Burnside Road, Victoria, British Columbia, Canada V8Z 1M5

ARTICLE INFO

Article history:
Received 12 July 2011
Received in revised form 14 January 2012
Accepted 17 January 2012
Available online 28 January 2012

Keywords:
Temperature
Development
Phenology
Maximum likelihood
Modeling
Population dynamics

ABSTRACT

The developmental response of insects to temperature is important in understanding the ecology of insect life histories. Temperature-dependent phenology models permit examination of the impacts of temperature on the geographical distributions, population dynamics and management of insects. The measurement of insect developmental, survival and reproductive responses to temperature poses practical challenges because of their modality, variability among individuals and high mortality near the lower and upper threshold temperatures. We address this challenge with an integrated approach to the design of experiments and analysis of data based on maximum likelihood. This approach expands, simplifies and unifies the analysis of laboratory data parameterizing the thermal responses of insects in particular and poikilotherms in general. This approach allows the use of censored observations (records of surviving individuals that have not completed development after a certain time) and accommodates observations from temperature transfer treatments in which individuals pass only a portion of their development at an extreme (near-threshold) temperature and are then placed in optimal conditions to complete their development with a higher rate of survival. Results obtained from this approach are directly applicable to individual-based modeling of insect development, survival and reproduction with respect to temperature. This approach makes possible the development of process-based phenology models that are based on optimal use of available information, and will aid in the development of powerful tools for analyzing eruptive insect population behavior and response to changing climatic conditions.

Crown Copyright © 2012 Published by Elsevier Ltd. All rights reserved.

1. Introduction

The physiological responses of organisms to temperature have had considerable attention in the scientific literature for more than a century. Recently, debate focused on a Metabolic Theory of Ecology (MTE) where temperature and body weight are the fundamental determinants of the rates at which life's central processes occur: metabolism, development, reproduction, population growth, species diversity and even ecosystem processes (Brown et al., 2004). Discussion centers around the existence of a Universal Temperature Dependence (UTD), in the form of the exponential Arrhenius equation $r = b_0 \exp(-E/kT)$ where r is some rate, b_0 is a proportionality constant that varies between processes and taxa, $E \approx 0.6$ to $0.7\ \mathrm{eVK}^{-1}$ is a near-constant activation energy, and $k = 8.6173 \times 10^{-5}\ \mathrm{eVK}^{-1}$ is the Boltzmann constant relating energy to temperature, K (°K). Arguments have centered on the validity and universality of the UTD (Clarke, 2006; Clarke and Fraser, 2004; Huey and Kingsolver, 2011) and the constancy and ecological correlates of its main parameter E (Dell et al., 2011; Irlich et al., 2009). The UTD provides an adequate description of biological rate responses over a limited range of temperatures but over the range of temperatures to which poikilotherms such as insects are exposed, responses to temperature are unimodal (Sharpe and DeMichele, 1977; Knies and Kingsolver, 2010). Consequently, the breadth of temperature range, thresholds and optimum temperatures at which this unimodality is expressed, as well as their variability are critical (Angilletta et al., 2002; de Jong and van der Have, 2009; Dixon et al., 2009).

For cold-blooded organisms, including insects, the relationships between ambient temperature and development, survival and reproduction scale up from daily or even hourly effects on individuals to seasonal patterns of phenology (Schwartz, 1998; Visser and Both, 2005), population dynamics (Logan et al., 2006; Yang and Rudolf, 2010), and species distributions including the expanding

* Corresponding author. Tel.: +1 418 648 5257; fax: +1 418 648 5849.
E-mail addresses: Jacques.Regniere@NRCan.gc.ca (J. Régnière), jim.powell@usu.edu (J. Powell), bbentz@fs.fed.us (B. Bentz), vince.nealis@nrcan.gc.ca (V. Nealis).

0022-1910/$ - see front matter Crown Copyright © 2012 Published by Elsevier Ltd. All rights reserved.
doi:10.1016/j.jinsphys.2012.01.010

interest in responses to climate change (Bentz et al., 2010; Kramer et al., 2000; Powell and Logan, 2005; Régnière and Logan, 2003; Sparks and Carey, 1995). Models that aim to predict the effects of temperature on the outcomes of these processes must account for the nonlinear nature of the thermal responses involved (Régnière and Logan, 2003; Schaalge and van der Vaart, 1988; Smerage, 1988), as well as the intraspecific and intrapopulation variability in these responses.

The intrinsic variability of developmental rates among individuals within populations (*sensu* Yurk and Powell, 2010) influences the observed distribution of phenological events in those populations. Thermal responses are often asymmetrically distributed and as such they can alter the timing of life stages (Gilbert et al., 2004) and its demographic consequences (Bellows, 1986; Powell and Bentz, 2009). From mathematical descriptions of these distributions, simulation models can generate age or stage frequencies including survival and reproduction over time in response to temperature input regimes. The most commonly used model categories are distributed delays (Manetsch, 1976), cohort-based (Sharpe et al., 1977), and individual-based (Cooke and Régnière, 1996; DeAngelis and Gross, 1992; Grimm, 2008).

Three issues in the design and analysis of temperature response experiments used to estimate parameters of phenology models are: (1) analysis of development times or their inverse, development rates (Kramer et al., 1991); (2) estimation of development times at temperatures near thresholds (extremes) where excessive mortality or developmental abnormalities such as the inability to hatch from an egg may occur; and (3) the relationship between individual variation and average developmental rates (Régnière, 1984; Wagner et al., 1984) and reproductive responses (Régnière, 1983).

In this paper, we propose a formal methodological framework within which to design experiments and analyze data on insect development, survival and reproduction responses estimated from individuals observed living in controlled, but not necessarily constant, temperatures. Our framework allows: (1) the use of censored data, where observations are interrupted after a certain time; (2) parsing of variance contributions between individual (intrinsic) and lack-of-fit; and (3) more precise estimation of thresholds by the transfer of individuals between extreme and moderate temperatures. It expands, simplifies and unifies the analysis of laboratory data parameterizing the thermal responses of insects in particular and poikilotherms in general. We demonstrate this approach using simulated data, data from the literature on the eastern spruce budworm *Choristoneura fumiferana* (Clem.), the spruce budmoth *Zeiraphera canadensis* Nutuua and Freeman (Lepidoptera: Tortricidae), the melon fly *Bactrocera cucurbitae* (Coquilett) (Diptera: Tephritidae), as well as new data from the mountain pine beetle *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae, Scolytinae) and the western spruce budworm *C. occidentalis* Freeman (Lepidoptera: Tortricidae).

2. Theory

2.1. Rate-summation models of insect development

The development rates of insects are rarely measured directly. Instead, they are calculated as the inverse of observed development time, such as the number of days between oviposition and hatch or between successive larval moults, and are expressed as proportions of total stage duration per unit of time. Development time and rate are related by:

$$\tau(T,\mathbf{A}) = \frac{1}{r(T,\mathbf{A})}, \tag{1}$$

where $\tau(T,\mathbf{A})$ represents the modeled average time required to complete the life stage at temperature T, and $\mathbf{A}$ is a vector of parameter values of temperature-response function $r(T,\mathbf{A})$. To model development under fluctuating temperature regimes, it is necessary to sum (integrate) development rates over short time steps, Δt, usually of a day or less (Régnière and Logan, 2003). This sum represents within-stage physiological age, a (proportion of the stage completed, from 0 at the onset to 1 at completion):

$$a_t = \int_0^t r(T_t,\mathbf{A})dt \cong \sum_0^t r(T_t,\mathbf{A})\Delta t. \tag{2}$$

As defined here, a is analogous to the physiological time scale defined by van Straalen (1983) under the assumption of linear development responses (see de Jong and van der Have, 2009).

2.2. Developmental responses to temperature and distributions

Many functions describe the developmental responses of insects to temperature. They can be classified in order of complexity, as represented by the number of parameters required. Seven functions are described in Table 1 (hereafter referred to as (A1)–(A7)). Of these, the Sharpe–Schoolfield model (A7) (Sharpe and DeMichele, 1977; Schoolfield et al., 1981) is the most "mechanistic" as it is based on enzyme kinetics. It is related to the UTD as it incorporates the Arrhenius equation (see De Jong and van der Have, 2009). Many of the other functions in Table 1 are simpler empirical mathematical descriptions of the shape of the temperature responses without a true mechanistic basis.

Let t_{ij} represent the development time of individual i in treatment j at constant temperature T. Index j could be a temperature treatment, replicate, sub-population, or some other sample unit of the experimental design. There are two sources of variation that make $t_{ij} \neq \tau(T,\mathbf{A})$. First, individuals vary in their responses to temperature. Second, additional sources of variation are pooled together as lack-of-fit between the theoretical thermal response, $\tau(T,\mathbf{A})$, and the true mean (or expected) development time, $E(t_j)$. If we define an individual's deviation from $E(t_j)$ as δ_{ij}, and the lack-of-fit between theoretical response and treatment mean, υ_j, we get:

$$t_{ij} = \delta_{ij}\upsilon_j\tau(T,\mathbf{A}). \tag{3}$$

This formulation assumes that the distribution of development time among individuals does not vary with temperature but that its variance is proportional to the square of the mean. Various functions have been used to describe this distribution based on their flexibility or simplicity (Dangles et al., 2008; Régnière, 1984; Stinner et al., 1975; Wagner et al., 1984; Yurk and Powell, 2010). We favor the lognormal distribution for three reasons. It ensures that $\delta \geqslant 0$, which is consistent with the fact that rates can only be $\geqslant 0$ in all individuals at all temperatures (development cannot regress). It is asymmetrical with a more or less pronounced positive skew (longer right-hand tail), which is a characteristic often observed in the distributions of both development times and development rates in insects (Curry et al., 1978). And it can be inverted without consequence (if ε is normally-distributed then $\delta = e^{\varepsilon}$ and $1/\delta = e^{-\varepsilon}$ are both lognormally-distributed), the error structure is the same whether variability is expressed as development times or development rates. Thus:

$$\varepsilon_{ij} = \ln\{t_{ij}/[\upsilon_j\tau(T,\mathbf{A})]\}, \tag{4}$$

is a normally-distributed random variable with mean $\mu_\varepsilon = -1/2\sigma_\varepsilon^2$ and variance σ_ε^2 (the skew of the lognormal distribution requires a non-zero μ_ε so that $E(\delta_{ij}) = 1$; Hilborn and Mangel, 1997). Because it is based on an expected value (a mean), the lack-of-fit term,

$$\upsilon_j = E(t_j)/\tau(T,\mathbf{A}), \tag{5}$$

can be assumed to be a multiplicative normally-distributed random effect with mean 1 and variance σ_υ^2 that is random with respect to treatment.

Table 1
Selected temperature-dependent development rate equations.

	Formulation	Validity range	Parameters	Source
(A1)	$r(T) = \psi e^{-\frac{1}{2}[(T-T_o)/\Delta_o]^2}$	$T > -273$	3	Taylor (1981)
(A2)	$r(T) = \psi T(T-T_b)(T_m-T)^{\omega}$	$T_b \leqslant T \leqslant T_m$	4	Brière et al. (1999)
(A3)	$r(T) = \psi\left[\frac{2(T-T_b)^{\alpha}(T_o-T_b)^{\alpha}-(T-T_b)^{2\alpha}}{(T_o-T_b)^{2\alpha}}\right]$ where $\alpha = \ln 2/\ln[(T_m-T_b)/(T_o-T_b)]$	$T_b \leqslant T \leqslant T_m$	4	Wang and Engel (1998)
(A4)	$r(T) = \psi\left[\frac{(T-T_b)^2}{(T-T_b)^2+\kappa} - e^{-\frac{T_m-(T-T_b)}{\Delta_m}}\right]$	$T_b \leqslant T \leqslant T_m$	4	Hilbert and Logan (1983)
(A5)	$r(T) = \psi\{[e^{\omega(T-T_b)}-1]-[e^{\omega(T_m-T_b)}-1]e^{-(T_m-T)/\Delta_m}\}$	$T_b \leqslant T \leqslant T_m$	5	Hansen et al. (2011)
(A6)	$r(T) = \psi\left[e^{\omega(T-T_b)} - \left(\frac{T_m-T}{T_m-T_b}\right)e^{-\omega(T-T_b)/\Delta_b} - \left(\frac{T-T_b}{T_m-T_b}\right)e^{\omega(T_m-T_b)-(T_m-T)/\Delta_m}\right]$	$T_b \leqslant T \leqslant T_m$	6	This paper
(A7]	$r(T) = \frac{\rho_{25}\frac{T_K}{298}\exp\left[\frac{H_A}{R}\left(\frac{1}{298}-\frac{1}{T_K}\right)\right]}{1+\exp\left[\frac{H_L}{R}\left(\frac{1}{T_L}-\frac{1}{T_K}\right)\right]+\exp\left[\frac{H_H}{R}\left(\frac{1}{T_H}-\frac{1}{T_K}\right)\right]}$ where T_K is temperature in temperature in °K and $R = 1.987$	$T > -273$	6	Schoolfield et al. (1981)

2.3. Parameter estimation by maximum likelihood

Unimodal development response functions can be fit to observations by least-squares regression using mean or median rates or times as dependent variables. Variability is described by fitting some empirical distribution to deviations between observed individual and predicted values (see Wagner et al., 1991). Alternatively, models with intrinsic distributions can be fit to individual data by maximum likelihood (Hansen et al., 2011; Yurk and Powell, 2010). Here, we formalize and generalize this approach.

Observations of development are made at intervals of dt days. So, the probability that individual i in treatment j at constant temperature T_j completes a stage during the observation interval $[t-dt, t]$ is:

$$q_{ij}(\sigma_\varepsilon, \sigma_\upsilon, \mathbf{A}) = f(\upsilon_j)\left\{F\left[\ln\left(\frac{t}{\upsilon_j\tau(T_j,\mathbf{A})}\right)\right] - F\left[\ln\left(\frac{t-dt}{\upsilon_j\tau(T_j,\mathbf{A})}\right)\right]\right\}, \tag{6}$$

where F is the cumulative normal probability distribution with variance σ_ε^2 and mean $-1/2\sigma_\varepsilon^2$ and f is the normal probability density function with variance σ_υ^2 and mean 1. The negative log likelihood (LL) to be minimized is:

$$LL(\sigma_\varepsilon, \sigma_\upsilon, \mathbf{A}) = -\sum_i\sum_j \ln[q_{ij}(\sigma_\varepsilon, \sigma_\upsilon, \mathbf{A})]. \tag{7}$$

The set of parameter values $\mathbf{A}$, σ_δ and σ_υ that minimize LL can be found through iterative optimization routines such as Procedure NLMIXED of SAS (see Appendix A for suggested SAS code). While the details of Eq. (6) are specific to the normal distribution assumed for υ and the lognormal distribution for δ (see Eq. (4)), its general form (probability of a value of υ times the difference in cumulative probabilities of δ between two successive observations) applies to whichever distribution is most appropriate. Also, there is no requirement that the observation interval be constant. It could vary from treatment to treatment or even between individuals.

2.3.1. Censored data

Observations at cool temperatures where development is slow may end before the stage is completed but while individuals are still alive. These constitute censored observations and we know that the actual development time is at least as long as the period when observations were censored. These censored data can be used in parameter estimation. Because we cannot estimate the mean development time in a treatment that contains censored observations, we assume that $\upsilon = 1$ for that treatment. The likelihood that an individual would complete its development in more than t_{ij} is simply $1 - F(\varepsilon_{ij}, \mathbf{A})$, where ε_{ij} is defined by (4). Thus, when censored observations are present, the general likelihood, whether censored or not, is given by:

$$l_{ij}(\sigma_\varepsilon, \sigma_\upsilon, \mathbf{A}) = (1-d_{ij})q_{ij}(\sigma_\varepsilon, \sigma_\upsilon, \mathbf{A}) + d_{ij}[1-F(\varepsilon_{ij}, \mathbf{A})], \tag{8}$$

where

$$d_{ij} = \begin{cases} 0 & \text{if not censored} \\ 1 & \text{if censored} \end{cases} \tag{9}$$

and the negative log likelihood to be minimized is:

$$LL(\sigma_\varepsilon, \sigma_\upsilon, \mathbf{A}) = -\sum_i\sum_j \ln[l_{ij}(\sigma_\varepsilon, \sigma_\upsilon, \mathbf{A})]. \tag{10}$$

2.3.2. Temperature transfers (near-threshold development)

Threshold temperatures are an idealized characteristic of development responses in the sense that they are not actually measured. In degree-day models, for example, the lower threshold temperature is estimated by extrapolation of the linear portion of the development-rate response data (Bergant and Trdan, 2006; Honek and Kocourek, 1990). Critical development times near the lower or upper temperature extremes, however, are notoriously difficult to estimate because most insects die before completing their development. Nevertheless knowledge of development rates at near-threshold temperatures is important to accurately predict development under fluctuating temperatures (de Jong and van der Have, 2009). This is especially true when using models to predict phenological events when seasonal temperatures hover near the lower threshold temperature (Worner, 1991, 1992).

To obtain reliable estimates of development time near such extremes, insects can be exposed first to a near-threshold temperature (T_1) for a fixed amount of time (t_1); short enough to avoid excessive mortality but long enough for significant development to occur, and then transferred to another temperature (T_2) to record the time $t_{2,i}$ required by individual i to complete the stage under more optimal conditions. For individuals involved in such transfer treatments, development is complete when:

$$\frac{t_{1,j}}{\delta_{ij}\upsilon_j\tau(T_1,\mathbf{A})} + \frac{t_{2,ij}}{\delta_{ij}\upsilon_j\tau(T_2,\mathbf{A})} = 1. \tag{11}$$

By rearranging (11), we get:

$$\varepsilon_{ij} = \ln\left(\frac{t_{1,j}}{\upsilon_j\tau(T_1,\mathbf{A})} + \frac{t_{2,ij}}{\upsilon_j\tau(T_2,\mathbf{A})}\right), \tag{12}$$

and Eq. (6) becomes

$$q_{ij}(\sigma_\varepsilon, \sigma_\upsilon, \mathbf{A}) = f(\upsilon_j)\left\{F\left(\ln\left[\frac{t_{1,j}}{\upsilon_j\tau(T_1,\mathbf{A})} + \frac{t_{2,ij}}{\upsilon_j\tau(T_2,\mathbf{A})}\right]\right) - F\left(\ln\left[\frac{t_{1,j}}{\upsilon_j\tau(T_1,\mathbf{A})} + \frac{t_{2,ij}-dt}{\upsilon_j\tau(T_2,\mathbf{A})}\right]\right)\right\}$$

where F is the cumulative normal probability distribution with variance σ_ε^2 and mean $-1/2\sigma_\varepsilon^2$ and f is the normal probability density

function with variance σ_υ^2 and mean 1. Note that Eq. (6) is a special case of Eq. (13) where $t_1 \equiv 0$ (no transfer treatment), and that Eq. (13) can represent the $q_{ij}(\sigma_\varepsilon, \sigma_\upsilon, \mathbf{A})$ term in Eq. (8) to estimate the parameter set $\mathbf{A}$, σ_δ and σ_υ when a design includes both censored and transfer treatment data (see Appendix A for an example of SAS code).

2.3.3. Modeling from means and sample sizes

A developmental response curve, and the associated variability, can be fit to mean development times ($\bar{t}_j$) and their associated sample sizes (n_j) by maximum likelihood even when data for individuals are not available. Using the definitions, notation and assumptions of Eq. (3), the mean of each treatment j is described by:

$$\bar{t}_j = \bar{\delta}_j \upsilon_j \tau(T_j, \mathbf{A}) \tag{14}$$

where $\bar{\delta}_j = \sum_i \delta_{ij}/n_j$. While δ_{ij} are lognormally distributed, their mean is approximately normally distributed because of the central limit theorem and we get:

$$\bar{\delta}_j = \frac{\bar{t}_j}{\upsilon_j \tau(T_j, \mathbf{A})} \sim \mathrm{N}\left(1, \frac{\sigma_\delta^2}{n_j}\right) \tag{15}$$

with $\upsilon_j \sim \mathrm{N}(1, \sigma_\upsilon^2)$. When treatment j involves a temperature transfer from T_{1j} for t_{1j} days, to temperature T_{2j} for the remainder of development (averaging $\bar{t}_{2j}$), this becomes:

$$\bar{\delta}_j = \frac{t_{1j}}{\upsilon_j \tau(T_{1j}, \mathbf{A})} + \frac{\bar{t}_{2j}}{\upsilon_j \tau(T_{2j}, \mathbf{A})}. \tag{16}$$

The probability of observing mean development time $\bar{t}_j$ (or $\bar{t}_{2j}$ with temperature transfers) is:

$$q_j(\sigma_\delta, \sigma_\upsilon, \mathbf{A}) = f(\upsilon_j) f(\bar{\delta}_j) \tag{17}$$

where f is the normal probability density function, with mean 1 and variance σ_υ^2 or σ_δ^2/n_j. The negative log likelihood to be minimized is:

$$LL(\sigma_\delta, \sigma_\upsilon, \mathbf{A}) = -\sum_j \ln[q_j(\sigma_\delta, \sigma_\upsilon, \mathbf{A})] \tag{18}$$

(see Appendix B for sample SAS code). Because the distribution of individual variation is assumed to be lognormally distributed (i.e., $\delta = e^\varepsilon$), where $\sigma_\delta^2 = e^{\sigma_\varepsilon^2} - 1$, we get:

$$\sigma_\varepsilon^2 = \ln(\sigma_\delta^2 + 1) \tag{19}$$

2.4. Modeling oviposition

In many species, cumulative oviposition follows a pattern of diminishing returns; the daily rate of oviposition declines with age. We assume that females oviposit a constant proportion, λ, of their remaining fecundity, F_t, per unit of time. This proportion can be a function of temperature, $\lambda(T, \mathbf{B})$, with set of parameters $\mathbf{B}$. Under these assumptions, the oviposition rate is:

$$\frac{dF_t}{dt} = -\lambda(T, \mathbf{B}) F_t. \tag{20}$$

Females may also have a pre-oviposition period, t_0, during which they mate, disperse, and complete maturation. Solving (20) at constant temperature T for this situation yields $F_t = F_0 e^{-\lambda(T,\mathbf{B})(t-t_0)}$, where F_0 is mean (potential) fecundity. We also assume lognormal variation in fecundity so that an individual's initial fecundity is $\eta_{ij} = e^{\varepsilon_{ij}}$, where $\varepsilon_{ij} \sim \mathrm{N}(\ln(F_0) - 1/2\sigma_\varepsilon^2, \sigma_\varepsilon^2)$. In many experiments, the number of eggs laid is measured on several occasions, indexed k, for each female throughout the interval $[t_{k-1}, t_k]$. The expected oviposition by individual ij during that interval is:

$$O_{ijk} = \eta_{ij}[e^{-\lambda(T_j,\mathbf{B})(t_{k-1}-t_0)} - e^{-\lambda(T_j,\mathbf{B})(t_k-t_0)}] \text{ for } t \geqslant t_0. \tag{21}$$

Parameters F_0, σ_ε and $\mathbf{B}$ can be estimated from these data by maximum likelihood. The number of eggs laid, E_{ijk}, by female ij during interval k is a Poisson variable with expected value O_{ijk}, and we get the probability of observing E_{ijk}:

$$q_{ijk}(\sigma_\varepsilon, \mathbf{B}) = f(\varepsilon_{ij}) \frac{O_{ijk}^{E_{ijk}} e^{-O_{ijk}}}{E_{ijk}!}, \tag{22}$$

where f is the normal probability density function with variance σ_ε^2 and mean $\ln(F_0) - 1/2\sigma_\varepsilon^2$. The negative log likelihood to be minimized is:

$$LL(\sigma_\varepsilon, \mathbf{B}) = -\sum_i \sum_j \sum_k \ln[q_{ijk}(\sigma_\varepsilon, \mathbf{B})]. \tag{23}$$

2.5. Modeling survival

In experiments designed to estimate development time using constant temperatures, survival during the life stage is commonly measured. Resulting observations of survival are typically modal with poorest survival at low and high temperatures. The causes of reduced survival near threshold temperatures can include heat or cold injury as well as bottlenecks when discrete developmental events such as egg hatch or larval moult cannot occur. These survival rates may be related to temperature by regression analysis. Predicting survival under variable temperatures requires calculation of mean temperature over the development period. Because of the strong unimodal non-linearity of the survival response, an approach similar to that used for development can be applied to survival data.

A parsimonious hypothesis is that life-stage survival at temperature T in treatment j is the simple result of exposure to a constant daily jeopardy that is a function of temperature, $\gamma(T_j, \mathbf{C})$, where $\mathbf{C}$ is a vector of parameter values. Survival over the duration of a given life stage in treatment j is:

$$S_j = \gamma(T_j, \mathbf{C})^{\bar{t}_j}, \tag{24}$$

where $\bar{t}_j$ is the average duration of the stage in treatment j or, if a treatment involves a temperature transfer:

$$S_j = \gamma(T_1, \mathbf{C})^{t_1} \gamma(T_2, \mathbf{C})^{\bar{t}_2}, \tag{25}$$

with temperatures T_1 and T_2 for times t_1 and $\bar{t}_2$ as defined earlier. The estimate of survival probability is based on average development time so the number of survivors, k_j, out of the initial number, n_j, in a treatment is a Poisson variable, with expected mean $n_j S_j$. The negative log likelihood to be minimized is:

$$LL(\mathbf{C}) = -\sum_j \ln\left[\frac{(n_j S_j)^{k_j} e^{-n_j S_j}}{k_j!}\right] \tag{26}$$

(see Appendix B for sample SAS code). When used in a variable temperature context, Eq. (24) becomes:

$$S_t = \prod_t \gamma(T_t, \mathbf{C})^{\Delta t}, \tag{27}$$

where Δt is the time step (fraction of a day). The stage-specific survival response to constant temperature is defined completely by replacing observed mean development times ($\bar{t}_j$) in Eq. (24) by the stage's developmental response function (Eq. (1)):

$$S = \gamma(T, \mathbf{C})^{\tau(T,\mathbf{A})}. \tag{28}$$

3. Materials and methods

3.1. Simulated dataset

To illustrate the analytical approach and test the efficacy of censoring and temperature transfer treatments on improving the qual-

ity of the thermal response functions obtained, we used a simulated dataset. First, we generated a "true" thermal response using Eq. (A6) with $\mathbf{A} = \{T_b = 5,\ \Delta_b = 0.1,\ T_m = 33,\ \Delta_m = 3,\ \omega = 0.13,\ \psi = 0.01\}$, $\sigma_\delta = 0.15$ and $\sigma_\upsilon = 0.1$. This function includes explicitly two developmental thresholds and their respective boundary regions (T_b, Δ_b: lower; T_m, Δ_m: upper). At temperatures $T = \{4, 8, 12, 16, 20, 24, 28, 32\ °C\}$, we applied lack-of-fit error by drawing values of $\upsilon \in N(1, \sigma_\upsilon^2)$ at random. This yielded three stochastically different mean development times $\upsilon\tau(T)$ for each temperature. From each mean, we drew a sample of 50 random values of $\varepsilon \sim N(-1/2\sigma_\delta^2, \sigma_\delta^2)$ to obtain $\delta = e^\varepsilon$ which were multiplied by their mean and rounded to the nearest day (the observation interval). This provided a sample of 1200 individual observations of development time $t = \text{round}[\delta\upsilon\tau(T, \mathbf{A}) + 0.5]$.

These data constituted the first "experiment"; censoring was applied to individuals with development times $\geqslant 75$ days. No individuals at 4 °C completed development prior to censoring and only a few were censored at 8 °C. In a second experiment, individuals were transferred to $T_2 = 16$ °C after $t_1 = 30$ days at 4 °C, $t_1 = 20$ days at $T_1 = 8$ °C or $t_1 = 6$ days at $T_1 = 32$ °C. No censoring was applied. The time required to complete development at 16 °C was calculated and rounded off to the nearest day to provide individual values of t_2.

We applied a constant, temperature-independent daily survival probability, $s = 0.98$ to make the dataset more realistic. Under these conditions, the probability of individual ij surviving to the end of its development is $P(\text{survival}) = s^{t_{ij}}$ for individuals kept at constant temperature, $P(\text{survival}) = s^c$ for censored observations ($c = 75$ in our example), and $P(\text{survival}) = s^{t_1}s^{t_2}$ for those in transfer treatments. The fate of individuals (survival or not) was set by drawing a uniformly distributed random number ξ in the range [0,1] for each and using $\xi \leqslant P(\text{survival})$ as the criterion for survival. The parameters of another model (Eq. (A7)) were estimated by maximum likelihood using these simulated data. This particular model was chosen because its complexity (six parameters) is similar to that of our "true" relationship. To start the numerical optimization procedure, initial parameter values that provided a reasonable fit to the data were chosen.

3.2. Western spruce budworm and spruce budmoth egg development

Individual egg masses (each containing about 20 eggs on average) of western spruce budworm (*C. occidentalis)* obtained from wild adult moths collected as pupae were placed in dry glass vials at seven constant temperatures (4.7, 8.7, 12.1, 15.6, 20.7 24.1 and 28.0 ± 1 °C). Egg masses were kept for 28–31 days at either 4.7 or 8.7 °C, and then transferred to 15.6 °C to hatch. Sample sizes ranged from 19 to 24 egg masses per temperature, except in the 4.7 °C treatment in which only 3 egg masses hatched. An additional 67 egg masses obtained from a diet-fed (McMorran, 1965) laboratory colony of *C. occidentalis* (Canadian Forest Service, Sault Ste. Marie, ON, Canada) were placed either at 5.1 °C for 30 days then transferred to 15.8 °C to complete development ($n = 34$) or were kept at 15.8 °C throughout ($n = 33$). Only 4/34 egg masses in this additional transfer treatment hatched, compared to 30/33 of those kept at 15.8 °C. Hatch was recorded daily. As individual eggs from spruce budworm egg masses hatch within minutes of each other, an egg mass was considered an individual in the analysis. This dataset ($n = 160$) provided an opportunity to test a variety of models using the same data. We tested Eqs. (A1)–(A7), and the best model was chosen on the basis of the corrected Akaike Information Criterion (AICc) that takes simultaneously into account the maximum likelihood, the number of parameters of the model and sample size.

Data on the duration of egg development of spruce budmoth *Z. canadensis* were taken from Table 1 in Régnière and Turgeon (1989). These data consist of the mean and sample size of development time from seven constant temperature treatments (7.6, 12, 16.3, 19.5, 23.4, 30 and 31.9 °C), plus two transfer treatments (32 or 38 days at $T_1 = 7.6$ °C, with development completed at $T_2 = 19.5$ °C). Data analysis followed the approach described in Eqs. (14)–(19), with Eq. (A7) as temperature-response model.

3.3. Mountain pine beetle development and oviposition

Time to complete each life stage of the mountain pine beetle (egg, four larval instars, pupa and teneral adult) was determined for populations collected in lodgepole pine (*Pinus contorta*) stands over several years from central Idaho and northern Utah, USA. Individuals were reared in 15 × 15 cm phloem sections sandwiched between plexiglass plates which enabled observation of changes in life stages (Bentz et al., 1991; Hansen et al., 2011) as follows. Mountain pine beetle-infested trees were felled and infested billets held in the laboratory to obtain emerging parent adults. Male–female pairs were inserted manually into un-infested billets of lodgepole pine. After 7-10 days eggs were collected and manually inserted into niches in phloem sandwiches. Sandwiches were kept in constant humidity desiccators in environmental chambers (Percival Scientific, Inc., Gray et al., 1998) at constant temperatures ranging from 4 to 27.5 °C. Larval moults were indicated by characteristic head capsule widths (Logan et al., 1998) and presence of the discarded head capsule of the previous stage. Development time of pupae and teneral adults at temperatures below the pupal threshold were determined by rearing individuals through the fourth instar at 20 °C and then placing the individual larvae within the phloem sandwich at the lower temperature. Completion of the teneral adult life stage was identified as the time when the new adult chewed out of the phloem sandwich. At low temperatures, observations were often censored because experiments stopped while individuals were still alive but had not yet moulted (e.g. 150 days). We tested Eqs. (A1)–(A7) using egg development times and selected the best model based on the AICc (this was (A[6]). We applied the same model to describe the developmental responses of all other stages. For the oviposition model, the number of eggs laid by 275 adult females was determined in experimentally infested billets after 1, and 10–16 days at eight constant temperatures between 7 and 24 °C (Amman, 1972).

3.4. Survival of melon fly eggs and spruce budworm larvae at constant temperature

To illustrate the use of Eqs. (24)–(28), we analyzed published data on survival of eggs of the melon fly (Messenger and Flitters, 1958, their Table 2) and spruce budworm larvae (Weber et al., 1999, their Tables 2 and 3). Melon fly egg hatch was observed hourly at 22 temperatures between 11.4 and 36.4 °C. The duration of larval development (from third instar to pupation) was measured daily for spruce budworm originating from six sites along a latitude gradient in Alberta, Canada, at 10 constant temperatures between 9.3 and 33 °C. Both datasets consist of the number of individuals reared and surviving, and the average development time at each temperature i (and from each population j in the case of spruce budworm).

For melon fly eggs, we used a 4th-degree polynomial in a logistic model of the form $\gamma(T, \mathbf{C}) = \mathbf{1}/[\mathbf{1} + \exp(\mathbf{a} + \mathbf{bT} + \mathbf{cT^2} + \mathbf{dT^3} + \mathbf{eT^4})]$ to describe the relationship between daily survival rate and temperature in Eq. (24). For spruce budworm larvae, a 2nd-degree polynomial was sufficient. However, to test for significant differences between source populations, we introduced in the analysis a random factor $\upsilon_k \in N(1, \sigma_\upsilon^2)$ associated with population k so that $\gamma_k(T, \mathbf{C}) = 1/[1 + \exp(a + bT + cT^2)] + \upsilon_k$ in Eq. (24).

Table 2
Parameter estimates (±standard error) and maximum likelihood from simulated datasets fitted to Eq. (A7).

Parameter	Original	Censored at 75 days	With transfers
ρ_{25}	0.119 ± 0.004	0.119 ± 0.004	0.121 = 3 ± 0.004
H_A	19764 ± 978	19764 ± 867	19764 ± 898
H_L	−60000 ± 9	−60000 ± 7	−60000 ± 27
T_L	265.6 ± 104.9	272.1 ± 5.6	278.3 ± 0.7
H_H	100017 ± 34	100017 ± 28	100017 ± 36
T_H	303.2 ± 0.2	303.2 ± 0.2	303.1 ± 0.2
σ_ε	0.153	0.155	0.159
σ_υ	0.077 ± 0.015	0.077 ± 0.014	0.075 ± 0.015
LL	−1653.8	−1565.1	−1774.0
AIC	3323.5	3146.3	3564.0

In both examples, the full survival response to temperature was obtained by fitting Eq. (A7) to mean development times and sample sizes to describe the development time responses to temperature $\tau(T, \mathbf{A})$ in Eq. (28). The data and SAS code used to conduct the analysis of spruce budworm survival are in Appendix B.

4. Results

4.1. Simulated dataset

The maximum likelihood estimation algorithm converged easily in all cases to provide very good parameter estimates to Eq. (A7) for both the censored and the temperature-transfer datasets (Fig. 1a and b; Table 2). Both methods resulted in much higher survival in the low-temperature treatments than if individuals had been allowed to complete their development without censoring or temperature transfers (Fig. 1c). There was not much difference in the quality of development rate estimates at temperatures ⩾8 °C. However, neither the censored nor uncensored data provided enough information to estimate accurately the lower threshold temperature represented by parameter T_L (uncensored: 265.6 ± 104.9°K; censored: 272.1 ± 5.6°K), while the temperature-transfer treatment from 4 to 16 °C allowed the model to estimate a much more realistic lower threshold of T_L = 278.3 ± 0.7 K (5.3 °C compared with the "true" value of 5 °C) (inset, Fig. 1b). The upper threshold, beyond which development rates drop sharply, was estimated well with all three datasets at T_H = 303.1 to 303.2 ± 0.3°K (30.1–30.2 °C). Estimates of variances were close to the true values in all cases. The maximum likelihood method estimated σ_ε = 0.153 to 0.159 and σ_υ = 0.075 to 0.077 compared with the "true" values of σ_ε = 0.15 and σ_υ = 0.1.

4.2. Western spruce budworm and spruce budmoth egg development

Western spruce budworm egg development data were described by all seven models tested and convergence of the iterative optimization was obtained easily in all cases. This dataset contained data from transfer treatments between the three lower temperatures (4.7, 5.1 and 8.7 °C) and 15.6 or 15.8 °C. The highest likelihood and lowest AICc were obtained with Eq. (A2) (Table 3; Fig. 2a and b). There was no relationship between model negative log-likelihood and the estimate of σ_ε. However, the lack-of-fit term σ_υ varied considerably and was lowest with the best-fitting model (Fig. 3a), a relationship that illustrates the importance of including lack-of-fit variance σ_υ so that the estimate of individual variation σ_δ is not artificially inflated by a poorly-fitting model.

Spruce budmoth egg development data were very well described by Eq. (A7) (Fig. 2c and d) with parameters ρ_{25} = 0.117 ±

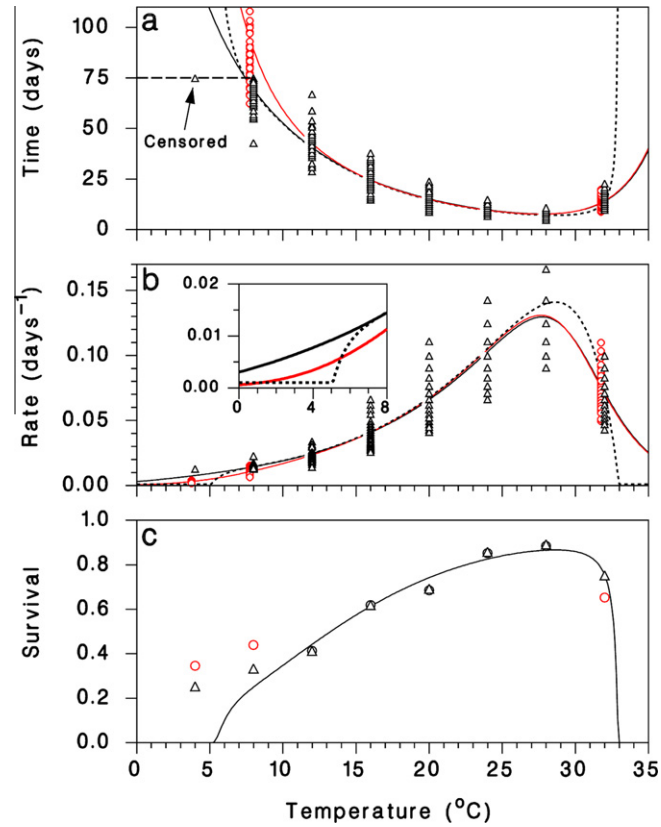

Fig. 1. Illustration of simulated censored and temperature-transfer datasets, and of analysis results. (a) Development time and (b) development rate: dotted line: "true" response (Eq. (A6)); solid black line: Eq. (A7) fitted to 75-day censored dataset. Red line: Eq. (A7) fitted to transfer-treatment dataset (no censoring). Inset: higher-resolution view of the lower temperature threshold. (c) Survival; line is survival in the absence of censoring or transfer treatments. △: Simulated data (constant temperature); ○: transfer treatments.

Table 3
Comparison of the best fit between seven models and the western spruce budworm egg development dataset. The best model was Eq. (A2), as illustrated in Fig. 2.

Parameter	(A1)	(A2)	(A3)	(A41)	(A5)	(A6)	(A7)
1	T_o = 29.7	T_b = 5.5	T_b = .5	T_b = 2.0	T_b = 0.0	T_b = 7.2	ρ_{25} = 0.158
2	Δ_o = 9.5	T_m = 41.5	T_m = 39.8	T_m = 43.0	T_m = 34.6	Δ_b = 1.7	H_A = 11443
3	ψ = 0.19	ω = 0.643	T_o = 30.0	Δ_m = 4.78	Δ_m = 5.9	T_m = 39.9	T_L = 283.9
4		ψ = 0.000055	ψ = 0.189	κ = 1861.4	ω = 0.141	Δ_m = 8.7	H_L = −59715
5				ψ = 0.761	ψ = 0.0231	ω = 0.109	T_H = 308.22
6						ψ = 0.0469	H_H = 99958
σ_ε	0.0645	0.0659	0.0653	0.0637	0.0640	0.0702	0.0627
σ_υ	0.0973	0.0830	0.0864	0.0716	0.0928	0.0836	0.0781
LL	−215.4	−212.0	−213.2	−213.4	−214.2	−212.1	−212.2
AIC	440.7	436.0	438.3	440.7	442.4	440.3	440.4
AICc	442.8	439.0	441.3	444.9	446.5	445.8	445.9
Parameters	5	6	6	7	7	8	8

0.012, $H_A = 13476 \pm 2176$, $H_L = -60076 \pm 144$, $T_L = 279.7 \pm 1.2$°K, $H_H = 59946 \pm 81$, $T_H = 303.8 \pm 3.0$°K and a small amount of lack-of-fit variation $\sigma_\upsilon = 0.03$. From the mean development times and sample sizes, we estimated $\sigma_\delta = 0.36$, or $\sigma_\varepsilon = 0.12$ (Eq. (19)). This dataset provides a good example of the use of temperature transfers to measure development rates at low temperatures. Estimates of development time and rate obtained from two different transfers between 7.6 and 19.5 °C compared very well with the measurements obtained from insects kept at 7.6 °C throughout their development (Fig. 2d).

4.3. Mountain pine beetle development and oviposition

Eq. (A6) provided the best fit, with the highest likelihood and lowest AICc for the mountain pine beetle egg development dataset (Table 4; Fig. 4a–c). As was the case with western spruce budworm egg development, there was no relationship between model goodness of fit and the estimate of σ_δ but there was a very definite one with the lack-of-fit term σ_υ (Fig. 3b). Slightly better fits based on the AICc were obtained with Eq. (A5) for a few other life stages but we used Eq. (A6) for all stages, including oviposition (Table 5; Fig. 4v–x), for the sake of consistency. The presence of censored data at lower temperatures in the egg (Fig. 4a and b) and larval stages helped considerably in determining the position of lower temperature thresholds (Fig. 4d, e, g, h, j and k; Tables 4 and 5). It is in the fourth instar that the lower development threshold was highest ($T_b = 16.2$ °C; $\Delta_b = 0.04$ °C), reflecting the conclusions of previous authors (Bentz et al., 1991; Powell et al., 2000) concerning the synchronizing role of the thermal response of this life stage in the seasonality and voltinism of the mountain pine beetle (Fig. 4m and n). The data for eggs and larval stages 1–3 provided sufficient evidence for the estimation of upper temperature thresholds (Fig. 4b, e, h and k). In the fourth instar, however, the absence of sufficient high temperature data forced us to limit this threshold to 28 °C to maintain consistency with the estimates obtained for the third instar and pupa (Fig. 4n). Teneral adults were observed evacuating the experimental set-ups at 8 and at 30 °C (Fig. 4s) which led to threshold estimates of $T_b = 4.2$ °C ($\Delta_b = 0.1$ °C) and $T_m = 35$ °C ($\Delta_m = 7.2$ °C; Fig. 4t). This emergence response differs from an adult flight threshold in the field which is estimated to be approximately 15.5 °C (Reid, 1962). Oviposition occurred at temperatures as low as 7 °C and the upper threshold was estimated at $T_m = 27.7$ °C ($\Delta_m = 3.1$ °C; Fig. 4w). According to the available data and the model being used, average fecundity was $F_0 = 81.8$ eggs per female. Our model suggests that in an unlimited phloem habitat, females can oviposit 95% of their eggs in 22 days at 24 °C (Fig. 4v).

The distribution of individual development rates around the expected mean was well approximated by the lognormal for all stages (Fig. 4 c, f, i, l, o, r, u and x), with the least variability among eggs ($\sigma_\varepsilon = 0.180$; Fig. 4c) and the most among teneral adults ($\sigma_\varepsilon = 0.528$; Fig. 4u).

4.4. Survival of melon fly eggs and spruce budworm larvae at constant temperature

Survival of melon fly eggs (data of Messenger and Flitters, 1958) was well described by the logistic equation:

$$S_j = \left(\frac{1}{1 + e^{a+bT+cT^2+dT^3+eT^4}}\right)^{\bar{t}_j}, \tag{29}$$

where $a = 151.1 \pm 10.9$, $b = -29.6 \pm 2.1$, $c = 2.03 \pm 0.14$, $d = -0.0592 \pm 0.0041$ and $e = 0.000625 \pm 0.000043$ (Fig. 5a). The developmental response to temperature was described accurately by Eq. (A7) (Fig. 5b), with parameters $\rho_{25} = 1.006 \pm 0.039$, $H_A =$

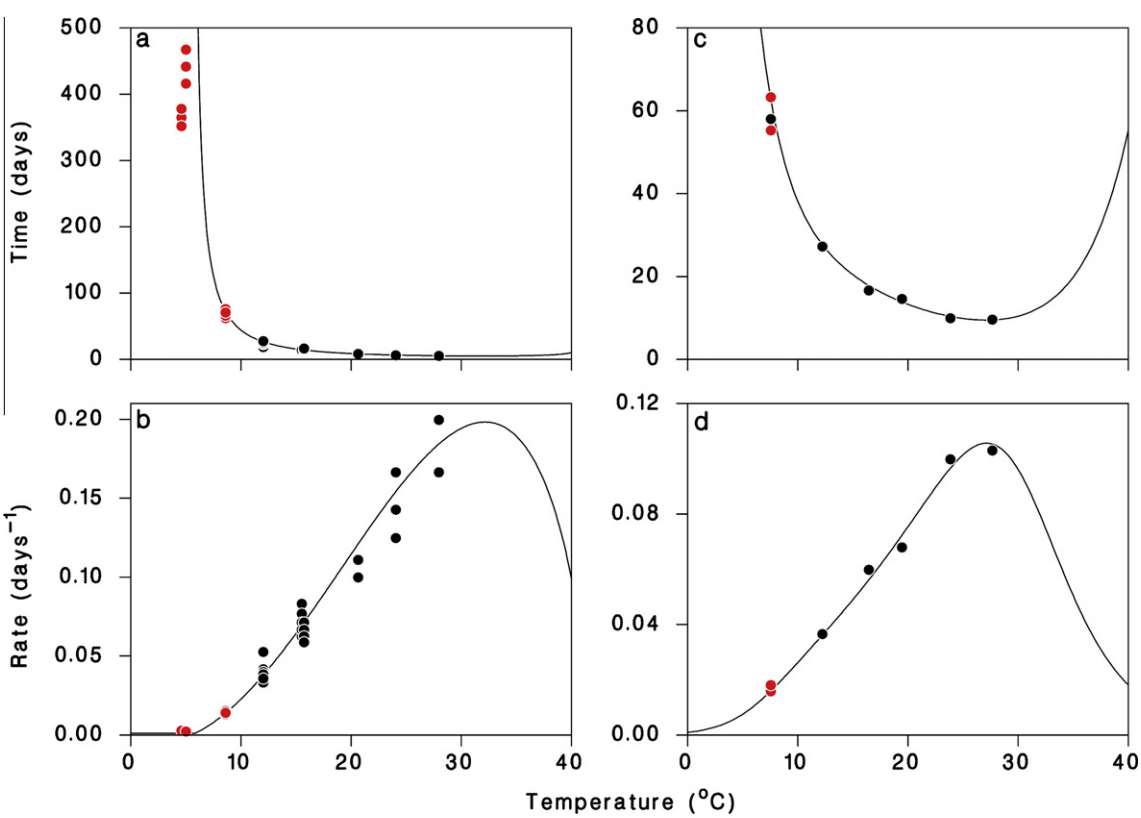

Fig. 2. Egg development data from two species of tortricids. Individual egg masses of western spruce budworm (a) development times and (b) development rates (Eq. (A2)). Average spruce budmoth egg (c) development times and (d) development rates (Eq. (A7)). ●: Constant temperature; ●: transfer treatments.

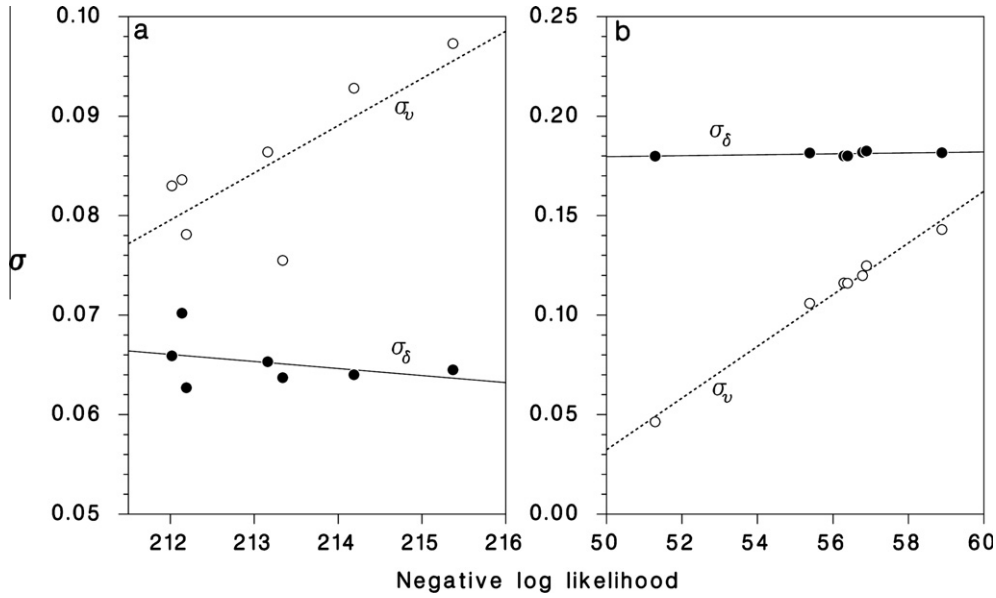

Fig. 3. Relationship between log likelihood (goodness of fit) and the σ_δ and σ_υ terms in Eq. (3) obtained by fitting various models to (a) western spruce budworm and (b) mountain pine beetle egg development. The estimates of σ_δ, the individual variation in development times, are stable from model to model, while the value of σ_ρ, the lack-of-fit term, appropriately increases as negative log likelihood increases.

6609 ± 1156, H_L = −41826 ± 1622, T_L = 289.8 ± 0.8°K, H_H = 147580 ± 9190, T_H = 309.0 ± 0.1°K, with σ_δ = 0.238 ± 0.036.

The influence of temperature on daily survival rates during the larval stages of the spruce budworm (data of Weber et al., 1999) was described by a second degree polynomial,

$$S_j = \left(\frac{1}{1+e^{a+bT+cT^2}} + \upsilon_k\right)^{\bar{t}_j}, \tag{30}$$

where a = −2.926 ± 0.504, b = −0.188 ± 0.055 and c = 0.00565 ± 0.00128 with very little variation due to source population (σ_υ = 0.00189 ± 0.00106, t_5 = 1.79, P = 0.13). These parameters indicate that temperatures in the range of 9.3–25 °C are optimal for the survival of this life stage (Fig. 5d). Lower daily survival rates were clearly observed at temperatures >25 °C. The effect of temperature on development time was well described by Eq. (A7) (Fig. 5e) with parameters ρ_{25} = 0.0636 ± 0.0089, H_A = 13476 ± 0, H_L = −34461 ± 11841, T_L = 281.8 ± 1.2°K, H_H = 49820 ± 14740, T_H = 305.4 ± 1.0°K, with σ_δ = 0.55 ± 0.05, and a vanishingly small amount of variation due to a population effect.

The overall survival responses to temperature that combine the equations for the parabolic response of daily survival with development time responses into Eq. (28) (Fig. 5c and f) illustrate the importance of exposure duration in explaining the deleterious effect of extreme temperatures on survival observed in typical constant-temperature experiments such as these. At both ends of the temperature-response scale (below 10 °C and above 30 °C in these examples), survival drops sharply because of a combination of increases in daily mortality and development time. These results also emphasize the usefulness of using temperature transfer treatments to estimate both survival and development rate near those temperature extremes to overcome the limitations imposed by constant experimental conditions.

5. Discussion and conclusions

Process-based phenology models for poikilotherms will have greater utility if they incorporate the entire biological consequences of physiological responses to temperature and use sufficient data to provide unbiased estimates of parameters. Improvements are particularly evident when simulating processes that occur at near-threshold temperatures where developmental responses are strongly nonlinear and measurements difficult to obtain. However, critical phenological events in the life history of organisms often occur when temperature regimes hover near these lower (or upper) thresholds (Worner, 1992); for example, resumption of spruce budworm development in the spring in temperate zones (Régnière et al., 2010). To incorporate these critical events into realistic simulations, the unimodal nature of developmental responses must be accommodated by the models and accurate data on development

Table 4
Comparison of the best fit between seven models and the mountain pine beetle egg development dataset. The best model was Eq. (A6).

Parameter	(A1)	(A2)	(A3)	(A4)	(A5)	(A6)	(A7)
1	T_o = 24.5	T_b = 2.7	T_b = 1.6	T_b = 1.6	T_b = 4.6	T_b = 7.0	ρ_{25} = 0.248
2	Δ_o = 7.6	T_m = 27.8	T_m = 37.2	T_m = 27.5	T_m = 28.7	Δ_b = 0.02	H_A = 16783
3	ψ = 0.194	ω = 0.148	T_o = 27.2	Δ_m = 0.675	Δ_m = 1.035	T_m = 30.1	T_L = 280.9
4		ψ = 0.000325	ψ = 0.197	κ = 1500	ω = 0.0538	Δ_m = 4.4	H_L = −69985
5				ψ = 0.831	ψ = 0.114	ω = 0.256	T_H = 301.1
6						ψ = 0.0237	H_H = 100003
σ_ε	0.182	0.180	0.183	.180	0.181	0.180	0.182
σ_υ	0.146	0.116	0.125	0.116	0.106	0.046	0.120
LL	58.9	56.3	56.9	56.4	55.4	51.3	56.8
AIC	127.8	124.7	125.9	126.9	124.8	118.7	129.7
AICc	128.6	125.9	127.1	128.6	126.5	120.8	131.9
Parameters	5	6	6	7	7	8	8

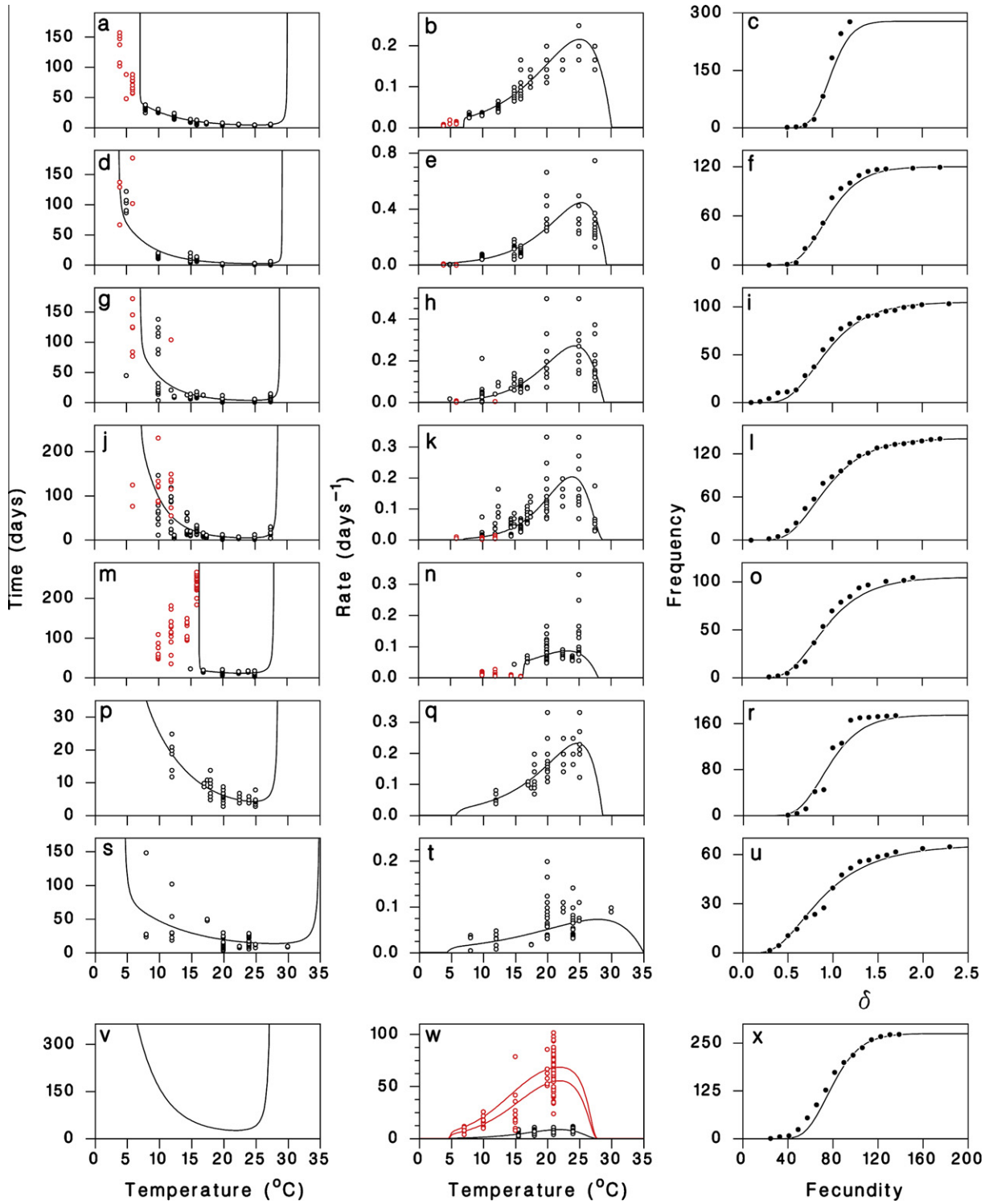

Fig. 4. Mountain pine beetle development and oviposition data fitted to Eqs. (A6) and (21). Left column: development time. Middle column: development rate. Right column: distribution of individual variation with corresponding lognormal distribution. ○: uncensored; ○: censored observations. Last row: oviposition; (v) time to lay 95% of total fecundity (days); (w) number of eggs laid on first day (○) and in first 10–16 days (○); (x) female fecundity η.

rates, survival and reproduction at several temperatures, including extremes, are essential to predicting phenological events in a fluctuating environment. Problems associated with measuring development near thresholds can be circumvented by including temperature transfer treatments between extreme and optimum temperatures in experimental designs with a sufficient proportion of the development taking place at the extreme temperature. Our approach shows that censored data can also be used to achieve better estimates.

The choice of an equation that describes adequately developmental responses to temperature should be based on evidence of unimodality in the data and prior information about the process being modeled but not contained in the data being analyzed, including thresholds. For actual unimodality to be apparent in

Table 5
Mountain pine beetle development and oviposition parameter estimates (Eqs. (A6) and (21)).

Parameter	L1	L2	L3	L4	Pupa	Teneral	Oviposition
T_b	3.6	7.0	6.8	16.2	5.6	4.2	4.6
Δ_b	0.1	0.10	0.10	0.04	0.11	0.10	0.10
T_m	29.3	28.9	28.7	28.0 (bound)	28.5	35 (bound)	27.8
Δ_m	3.8	3.0	2.5	4.6	2.9	7.1	3.1
ω	0.240	0.371	0.440	0.259	0.153	0.146	0.368
ψ	0.01082	0.00642	0.00389	0.0503	0.0205	0.0117	0.0052
σ_δ	0.2911	0.380	0.387	0.393	0.300	0.528	0.246
σ_υ	0.365	0.171	0.321	0.211	0	0.190	
F_0							81.8
LL	138.7	240.3	349.3	121.8	52.9	176.4	853.1

response data, a sufficient range and number of treatment temperatures must be available, especially for near-extreme temperatures (both cold and warm). Our analysis of mountain pine beetle development responses shows the importance of choosing an equation that can describe the important features of the data. For example, the use of Eq. (A6) allowed us to estimate precisely the lower developmental threshold temperatures of the larval stages of central importance to the synchronization of this insect's seasonality (Bentz et al., 1991; Powell et al., 2000).

Fitting complex equations using nonlinear least-squares and treatment means or medians often leads to issues of over-parameterization and convergence (Schoolfield et al., 1981). The solution is to increase the number of treatments. Temperature transfer treatments and the use of censored data make this possible, although convergence remains an issue when the analysis is based on maximum likelihood estimation. However, analyzing development time data in two steps, first by fitting a model with no lack-of-fit variance term and then by estimating σ_υ^2 using the results of that first step as initial parameter estimates, appears a good solution. Our maximum-likelihood method uses data from numerous individuals which increases the degrees of freedom available to estimate model parameters. However, this does not mean that it reduces the number of treatments needed because there remain inflection-points (thresholds) which sufficient data are essential to detect. There are two additional advantages of the maximum-likelihood approach. First it resolves the question of whether to fit an equation to development rates or development times. Likelihoods are based on the probability of observing life-stage transitions during each observation interval, and parameter estimation must be based on the observed times. Finally, having an explicit likelihood framework with common error assumptions allows comparison of multiple rate models, potentially representing different physiological hypotheses, via the AIC.

The incorporation of the structure of variation in development times and rates increases the power of process models. Results

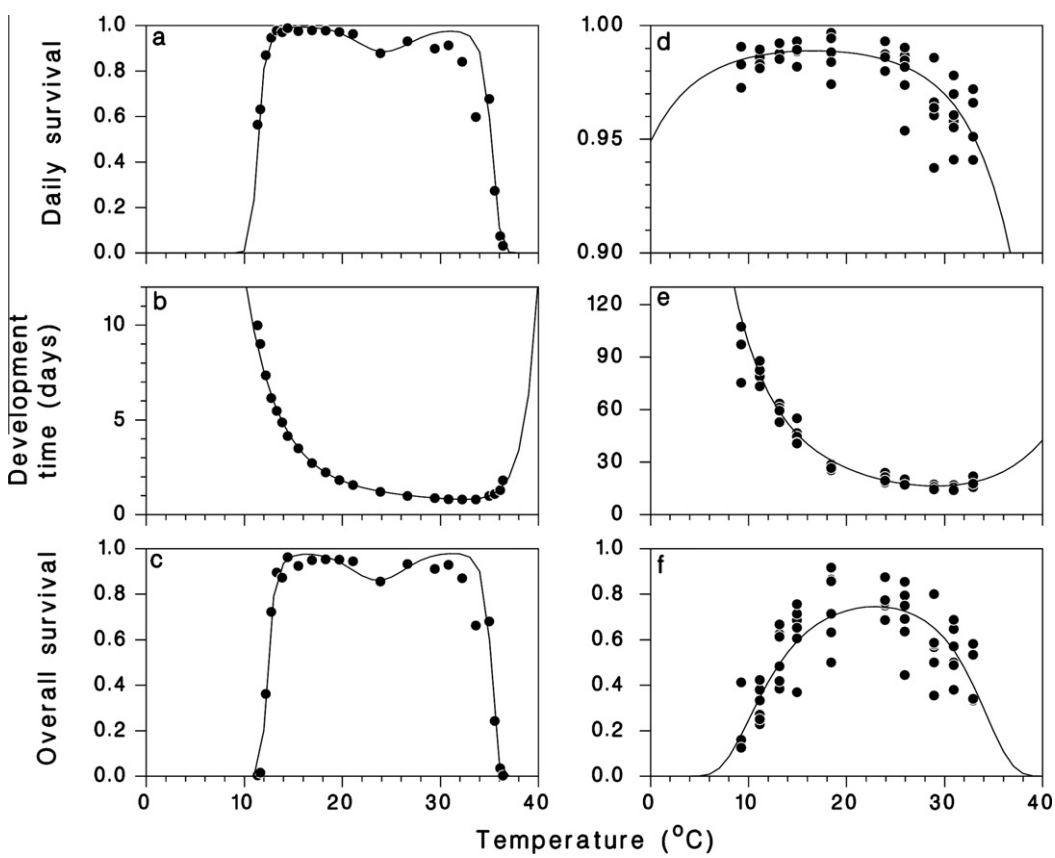

Fig. 5. Relationship between temperature and survival in (a–c) spruce budworm larvae (data of Weber et al., 1999) and (d–f) melon fly eggs (data of Messenger and Flitters, 1958). Daily survival rates described by (a) Eq. (30) and (d) Eq. (29). Mean development time (b and e) described by Eq. (A7). Overall survival (c and f) from Eq. (28).

obtained from the analysis methods described in this paper can be applied directly to two of these approaches: individual-based and cohort-based models. In individual-based models, development, survival and oviposition are simulated for a collection of individuals, each having its own assigned traits and going through successive life stages at its own individual pace. At initiation, each individual is assigned randomly different values of deviation from mean development time for each life stage, according to the lognormal distribution. Lack-of-fit variation, because of its extrinsic nature, is not modeled. Females in the reproductive stage are similarly assigned an initial fecundity at random. Survival of an individual during each time step is simulated by drawing a uniformly-distributed random number and removing the individual if this number is larger than the survival probability during that time step. One of the many advantages of the individual-based approach is the simplicity with which complex behaviors can be modeled. Among these, the transmission of traits from parent to progeny (e.g., development rates) offers the possibility of explicitly modeling natural selection. Constraints of individual-based models resulting from their high computing demands are diminishing with more powerful technology and the use of solutions such as parallel processing or amalgamating individuals into "super-individuals" that behave as cohorts (Parry and Evans, 2008; Yurk and Powell, 2010).

A second approach that models insects in groups or cohorts has been applied to many insect species (Curry et al., 1978; Logan, 1988). A cohort is a group of insects that enters a stage during a given time interval, ages according to Eq. (2), survives over time according to Eq. (27) and changes stage (passes to a new cohort) according to some probability distribution. These probabilities are determined by the cohort's stage and physiological age a within that stage. Sharpe et al. (1977) showed that the distributions of development rates and times are interchangeable. This is especially true if the distribution is lognormal as assumed since δ and $1/\delta$ have identical distributions. Cohort models tend to require less computing power than individual-based models although both depend equally on sample size. However, because individual traits are not distinguished in cohort-based models, they are not as useful to investigate evolutionary adaptation through the inheritance of individual traits as individual-based models.

Phenology models driven by functional relationships between insect development and ambient temperature are powerful tools for scaling life history events of insects over wide spatial and temporal scales and for analyzing insect responses to changing or novel climatic conditions and provide insight for ecological inquiries at the fine scale of host plant-insect synchrony and population dynamics and at the broad scale of geographic distribution of species (Bentz et al., 2010; Régnière et al., 2009, 2010; Safranyik et al., 2010). This makes possible the analytic prediction of temperature-dependent, emergent behavior in natural systems which are outside the scope of empirical models of observed trends. Our approach makes possible more accurate and robust phenology models based on the optimal use of available information, even when practical difficulties of obtaining measurements seem daunting. The predictive capacity of these models enables both the validation of the structure and the verification of predictions to increase confidence in our ability to anticipate and understand population changes in a variable and dynamic thermal environment.

We believe that the formulation of sound and complete ecological theory around thermal responses requires that these responses be completely described in terms not only of level (the b_0 parameter of the UTD), but also of shape and temperature range. For the results of such analyses to be comparable, it would also be helpful to use a common expression with as few parameters as possible. Perhaps the best candidate equation available at this time for this purpose is the Sharpe–Schoolfield model, Eq. (A7) (Sharpe and DeMichele, 1977; Schoolfield et al., 1981). This model has solid roots in enzyme thermodynamics and has been well studied (de Jong and van der Have, 2009). Its six parameters can be used to discuss the various critical aspects of species' thermal responses. Its use might facilitate the advancement of our understanding of the evolution of thermal physiology (Angilletta et al., 2002) and spatial patterns of fitness of ectotherms in response to climate (Deutsch et al., 2008). A database of parameter values obtained by the methods described here for as many species as possible would constitute a valuable contribution to such a discussion.

Acknowledgements

We thank Matt Hansen, Lynn Rasmussen and Jim Vandygriff for their assistance with mountain pine beetle phloem sandwich construction and phenology data collection. The USDA Forest Service (Rocky Mountain Research Station), Canadian Forest Service, Alberta Sustainable Development Department, the Ontario and Manitoba Ministries of Natural Resources, and Saskatchewan Environment provided funding for this research.

Appendix A. SAS code example, western spruce budworm egg development

```
data dataset;
  input T1 time1 T2 time2 n censored;
*observations are made on a daily basis at all temperatures;
  tm1 = time2 − 1;

  datalines;
4.7 28 15.6 12 1 0
4.7 30 15.6 11 1 0
4.7 30 15.6 12 1 0
5.1 30 15.8 15 1 0
5.1 30 15.8 16 2 0
5.1 30 15.8 17 1 0
8.7 30 15.6 7 1 0
8.7 30 15.6 8 8 0
8.7 30 15.6 9 4 0
8.7 30 15.6 10 1 0
8.7 31 15.6 7 3 0
8.7 31 15.6 8 1 0
8.7 31 15.6 9 1 0
12.1 0 12.1 19 1 0
12.1 0 12.1 24 3 0
12.1 0 12.1 25 5 0
12.1 0 12.1 26 5 0
12.1 0 12.1 28 6 0
12.1 0 12.1 30 1 0
15.6 0 15.6 12 1 0
15.6 0 15.6 13 7 0
15.6 0 15.6 14 6 0
15.6 0 15.6 15 7 0
15.6 0 15.6 16 3 0
15.8 0 15.8 14 5 0
15.8 0 15.8 15 15 0
15.8 0 15.8 16 8 0
15.8 0 15.8 17 2 0
20.7 0 20.7 9 9 0
20.7 0 20.7 10 10 0
24.1 0 24.1 6 1 0
24.1 0 24.1 7 17 0
24.1 0 24.1 8 3 0
```

```
28.0 0 28.0 5 4 0
28.0 0 28.0 6 15 0
;

*Data should be sorted by treatment (here T1) since upsilon is
  a treatment-level random effect;
  proc sort data = Dataset;
    by T1;
    run;

proc NLMIXED data = Dataset;
  Title "Sharpe–Schoolfield (A7)";
  parms
  rho25 = 0.16
  HA = 9831
  TL = 284.5
  HL = −59750
  TH = 307.9
  HH = 99935
  s_eps = .07
  s_upsilon = .03;

  bounds TL ⩾ 273, TH ⩽ 308, s_eps > 0, s_upsilon > 0;

  se2 = −0.5 * s_eps * s_eps;

*Development time at T1 (temperature transfers in the
  design);
  tK1 = T1 + 273;
  num = rho25 * tK1/298 * EXP(HA/1.987 * (1/298-1/tK1));
  den1 = EXP(HL/1.987 * (1/TL-1/tK1));
  den2 = EXP(HH/1.987 * (1/TH-1/tK1));
  tau = 1/(num/(1 + den1 + den2));
  tpred1 = upsilon * tau;

*Development time at T2 (temperature transfers in the
  design);
  tK2 = T2 + 273;
  num = rho25 * tK2/298 * EXP(HA/1.987 * (1/298-1/tK2));
  den1 = EXP(HL/1.987 * (1/TL-1/tK2));
  den2 = EXP(HH/1.987 * (1/TH-1/tK2));
  tau = 1/(num/(1 + den1 + den2));
  tpred2 = upsilon * tau;

*For the purpose of estimation, avoid predicted times lower
  than 1 day;
  if(tpred1 < 1) then tpred1 = 1;
  if(tpred2 < 1) then tpred2 = 1;
*compute values of epsilon = log(delta);
  epsm1 = log(time1/tpred1 + tm1/tpred2);
  epsij = log(time1/tpred1 + time2/tpred2);

*Probability of epsilon ij (valid for all, including temperature
  transfers and censoring);
  p = (1-censored) * (cdf('normal',epsij,se2,s_eps)-
  cdf('normal',epsm1,se2,s_eps))
    +(censored) * (1-cdf('normal',epsij,se2,s_eps));
  if(p > 1e−10) then ll = log(p);
  else ll = log(1e−10);
  model epsij ~ general(n * ll);
  random upsilon ~ NORMAL(1,s_upsilon * s_upsilon)
  subject = T1;
run;
```

Appendix B. SAS code example, spruce budworm larval survival and development

```
data Weber_et_al_1999;
/*Data from Tables 2 and 3 in Weber, J. D., W. J. A. Volney, ans
  J. R. Spence. 1999.
  Environmental Entomology 28(2): 224-232*/
  input Pop T nT Time Surv n;
  Datalines;
1 9.3 2 107.5 4 25
1 11.2 9 83.4 11 29
1 13.2 13 60.2 14 29
1 15.0 23 44.5 24 35
1 18.5 35 25.4 38 44
1 24.0 16 24.1 21 28
1 26.0 30 17.4 31 39
1 29.0 13 15.4 21 37
1 31.0 10 14.3 22 34
1 33.0 4 22.3 16 30
2 11.2 8 78.9 10 37
2 13.2 5 63.6 10 26
2 15.0 19 46.7 25 35
2 18.5 13 28.9 15 21
2 24.0 18 18.8 24 35
2 26.0 13 18.8 18 24
2 29.0 8 16.1 11 31
2 31.0 3 16.0 11 29
3 9.3 2 75.5 2 16
3 11.2 8 79.0 10 30
3 13.2 13 60.8 15 24
3 15.0 20 44.7 23 38
3 18.5 21 29.2 22 24
3 24.0 16 21.4 22 29
3 26.0 35 20.3 38 55
3 29.0 15 17.3 31 62
3 31.0 11 16.2 23 46
3 33.0 5 15.8 25 43
4 11.2 12 82.7 22 52
4 13.2 29 61.2 38 62
4 15.0 22 41.1 31 41
4 18.5 37 28.6 42 49
4 24.0 10 21.6 13 17
4 26.0 40 16.5 41 48
4 29.0 17 15.9 32 40
4 31.0 19 17.0 33 48
4 33.0 2 22.0 11 33
5 11.2 7 87.9 8 35
5 13.2 14 59.6 18 43
5 15.0 28 40.8 30 46
5 18.5 29 28.7 31 49
5 24.0 44 18.5 48 62
5 26.0 12 17.2 16 36
5 29.0 14 16.0 22 38
5 31.0 15 15.7 21 43
5 33.0 5 17.8 18 53
6 9.3 6 97.3 7 17
6 11.2 2 73.5 3 12
```

(*continued on next page*)

```
6 13.2 6 53.0 8 12
6 15.0 7 55.1 7 19
6 18.5 10 26.7 10 20
6 24.0 7 19.6 7 8
6 26.0 11 17.2 14 22
6 29.0 12 14.6 17 29
6 31.0 7 14.0 12 21
;

proc sort data=Weber_et_al_1999;
  by pop T;
run;

/*****************************************************
    Analysis of survival rates
*****************************************************/
proc NLMIXED data = Weber_et_al_1999;
  Title "Weber et al (1999) survival rates (Eq. (24))";
  parms
    a = −4.9273
    b = −0.004754
    c = 0.000033
    s_upsilon = .1;
  bounds s_upsilon > 0;
  gamma = 1/(1 + exp(a + b * T + c * T ** 2));
  S = (gamma + upsilon) ** Time;
  expected = n * S;

  model surv ~ Poisson(expected);

*upsilon is a Pop random effect;
  random upsilon ~ NORMAL(0,s_upsilon * s_upsilon)
   subject = Pop;
run;

/*****************************************************
    Analysis of development times
*****************************************************/
proc NLMIXED data = Weber_et_al_1999;
  Title "Weber et al (1999) development times";
  parms
    rho25 = 0.117
    HA = 13476
    HL = −60076
    TL = 279.3
  HH = 59946
    TH = 304.1
    s_delta = .5
    s_upsilon = .1;

  bounds s_upsilon > 0, s_delta > 0;

/*Sharpe–Schoolfield Eq. (A7)*/
  TK = T + 273;
  num = rho25 * TK/298 * EXP(HA/1.987 * (1/298-1/TK));
  den1 = EXP(HL/1.987 * (1/TL-1/TK));
  den2 = EXP(HH/1.987 * (1/TH-1/TK));
  tau = 1/(num/(1 + den1 + den2));

  if(upsilon > 0) then delta_bar = time/(upsilon * tau);
  else delta_bar = 1000; /*Some non-sensical value*/

  model delta_bar ~ normal(1,s_delta * s_delta/n);
  random upsilon ~ normal(1,s_upsilon * s_upsilon)
   subject = Pop;
run;
```

References

Amman, G.D., 1972. Some factors affecting oviposition behavior of the mountain pine beetle. Environmental Entomology 1, 691–695.

Angilletta, M.J., Niewiarowski, P.H., Navas, C.A., 2002. The evolution of thermal physiology in ectotherms. Journal of Thermal Biology 27, 249–268.

Bellows Jr., T.S., 1986. Impact of developmental variance on behavior of models for insect populations I. Models for populations with unrestricted growth. Researches on Population Ecology 28, 53–62.

Bentz, B.J., Logan, J.A., Amman, G.D., 1991. Temperature-dependent development of the mountain pine beetle (Coleoptera: Scolytidae) and simulation of its phenology. The Canadian Entomologist 123, 1083–1094.

Bentz, B.J., Régnière, J., Fettig, C.J., Hansen, E.M., Hayes, J.L., Hicke, J.A., Kelsey, R.G., Negrón, J.F., Seybold, S.J., 2010. Climate change and bark beetles of the western United States and Canada: direct and indirect effects. BioScience 60, 602–613.

Bergant, K., Trdan, S., 2006. How reliable are thermal constants for insect development when estimated from laboratory experiments? Entomologia Experimentalis et Applicata 120, 251–256.

Brière, J.-F., Pacros, P., Le Roux, A.-Y., Pierre, J.-S., 1999. A novel rate model of temperature-dependent development for arthropods. Environmental Entomology 28, 22–29.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., West, G.B., 2004. Toward a metabolic theory of ecology. Ecology 85, 1771–1789.

Clarke, A., 2006. Temperature and the metabolic theory of ecology. Functional Ecology 20, 405–412.

Clarke, A., Fraser, K.P.P., 2004. Why does metabolism scale with temperature? Functional Ecology 18, 243–251.

Cooke, B.J., Régnière, J., 1996. An object-oriented, process-based stochastic simulation model of *Bacillus thuringiensis* efficacy against spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). International Journal of Pest Management 42, 291–306.

Curry, G.L., Feldman, R.M., Sharpe, P.J.H., 1978. Foundations of stochastic development. Journal of Theoretical Biology 74, 397–410.

Dangles, O., Carpio, C., Barragan, A.R., Zeddam, J.-L., Silvain, J.-F., 2008. Temperature as a key driver of ecological sorting among invasive pest species in the tropical Andes. Ecological Applications 18, 1795–1809.

de Jong, G., van der Have, T.M., 2009. Temperature dependence of development rate, growth rate and size: from biophysics to adaptation. In: Whitman, D.W., Ananthakrishnan, T.N. (Eds.), Phenotypic Plasticity of Insects: Mechanisms and Consequences. Science Publishers, Enfield, New Hampshire, pp. 523–588.

DeAngelis, D.L., Gross, L.J., 1992. Individual-based Models and Approaches in Ecology: Populations, Communities and Ecosystems. Chapman and Hall, New York.

Dell, A.I., Pawar, S., Savage, V.M., 2011. Systematic variation in the temperature dependence of physiological and ecological traits. Proceedings of the National Academy of Sciences 108, 10591–10596.

Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor, C.K., Haak, D.C., Martin, P.R., 2008. Impacts of climate warming on terrestrial ectotherms across latitude. Proceedings of the National Academy of Sciences 105, 6668–6672.

Dixon, A.F.G., Honek, A., Keil, P., Kotela, M.A.A., Sizling, A.L., Jarosik, V., 2009. Relationship between the minimum and maximum temperature thresholds for development in insects. Functional Ecology 23, 257–264.

Gilbert, E., Powell, J.A., Logan, J.A., Bentz, B.J., 2004. Comparison of three models predicting developmental milestones given environmental and individual variation. Bulletin of Mathematical Biology 66, 1821–1850.

Gray, D.R., Ravlin, F.W., Logan, J.A., 1998. Microprocessor-controlled mini-environmental chambers capable of subfreezing temperatures in constant or time-varying temperature regimes. The Canadian Entomologist 130, 91–104.

Grimm, V., 2008. Individual-based models. In: Jorgensen, S.E., Faith, B.D. (Eds.), Encyclopedia of Ecology, Ecological Models, vol. 3. Elsevier, Oxford, UK, pp. 1959–1968.

Hansen, E.M., Bentz, B.J., Powell, J.A., Gray, D.R., Vandygriff, J.C., 2011. Prepupal diapause and instar IV developmental rates of the spruce beetle, *Dendroctonus rufipennis* (Coleoptera: Curculionidae, Scolytinae). Journal of Insect Physiology 57, 1347–1357.

Hilbert, D.W., Logan, J.A., 1983. Empirical model of nymphal development for the migratory grasshopper, *Melanoplus sanguinipes* (Orthoptera: Acrididae). Environmental Entomology 12, 1–5.

Hilborn, R., Mangel, M., 1997. The ecological detective: confronting models with data. Monographs in Population Biology, vol. 28. Princeton University Press, Princeton, NJ.

Honek, A., Kocourek, F., 1990. Temperature and development time in insects: a general relationship between thermal constants. Zoologische Jahrbuecher Jena Systematik 117, 401–439.

Huey, R.B., Kingsolver, J.G., 2011. Variation in universal temperature dependence of biological rates. Proceedings of the National Academy of Sciences 108, 10377–10378.

Irlich, U.M., Terblanche, J.S., Blackburn, T.M., Chown, S.L., 2009. Insect rate-temperature relationships: environmental variation and the metabolic theory of ecology. American Naturalist 174, 819–835.

Knies, J.I., Kingsolver, J.G., 2010. Erroneous Arrhenius: modified Arrhenius model best explains the temperature dependence of ectotherm fitness. American Naturalist 176, 227–233.
Kramer, K., Leinonen, I., Loustau, D., 2000. The importance of phenology for the evaluation of impact of climate change on growth of boreal, temperate and Mediterranean forest ecosystems: an overview. International Journal of Biometeorology 44, 67–75.
Kramer, D.A., Stinner, R.E., Hain, F.P., 1991. Time versus rate in parameter estimation of nonlinear temperature-dependent development models. Environmental Entomology 20, 484–488.
Logan, J.A., 1988. Toward an expert system for development of pest simulation models. Environmental Entomology 17, 359–376.
Logan, J.A., Bentz, B.J., Vandygriff, J.C., Turner, D.L., 1998. General program for determining instar distributions from headcapsule widths: example analysis of mountain pine beetle (Coleoptera: Scolytidae) data. Environmental Entomology 27, 555–563.
Logan, J.D., Wolesensky, W., Joern, A., 2006. Temperature-dependent phenology and predation in arthropod systems. Ecological Modelling 196, 471–482.
Manetsch, T.J., 1976. Time-varying distributed delays and their use in aggregative models of large systems. IEEE Transactions on Systems, Man and Cybernetics 6, 547–553.
McMorran, A., 1965. A synthetic diet for the spruce budworm, *Chroristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae). The Canadian Entomologist 97, 58–62.
Messenger, P.S., Flitters, N.E., 1958. Effect of constant temperature environments on the egg stage of three species of Hawaiian fruit flies. Annals of the Entomological Society of America 51, 109–119.
Parry, H.R., Evans, A.J., 2008. A comparative analysis of parallel processing and super-individual methods for improving the computational performance of a large individual-based model. Ecological Modelling 214, 141–152.
Powell, J.A., Bentz, B.J., 2009. Connecting phenological predictions with population growth rates for mountain pine beetle, an outbreak insect. Landscape Ecology 24, 657–672.
Powell, J.A., Logan, J.A., 2005. Insect seasonality: circle map analysis of temperature-driven life cycles. Theoretical Population Biology 67, 161–179.
Powell, J.A., Jenkins, J.L., Logan, J.A., Bentz, B.J., 2000. Seasonal temperature alone can synchronize life cycles. Bulletin of Mathematical Biology 62, 977–998.
Régnière, J., 1983. An oviposition model for the spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). The Canadian Entomologist 115, 1371–1382.
Régnière, J., 1984. A method of describing and using variability in development rates for the simulation of insect phenology. The Canadian Entomologist 116, 1367–1376.
Régnière, J., Logan, J.A., 2003. Animal life cycle models. In: Schwartz, M.D. (Ed.), Phenology: An Integrative Environmental Science. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 237–254.
Régnière, J., Turgeon, J.J., 1989. Temperature-dependent development of *Zeiraphera canadensis* and simulation of its phenology. Entomologia Experimentalis et Applicata 50, 185–193.
Régnière, J., Nealis, V.G., Porter, K., 2009. Climate suitability and management of the gypsy moth invasion into Canada. Biological Invasions 11, 135–148.
Régnière, J., St-Amant, R., Duval, P., 2010. Predicting insect distributions under climate change from physiological responses: spruce budworm as an example. Biological Invasions. doi:10.1007/s10530-010-9918-1.
Reid, R.W., 1962. Biology of the mountain pine beetle, Dendroctonus monticolae, in the east Kootenay region of British Columbia. I. Life cycle, brrod development and flight thresholds. Canadian Entomologist 94, 531–538.
Safranyik, L., Carroll, A.L., Régnière, J., Langor, D.W., Riel, W.G., Shore, T.L., Peter, B., Cooke, B.J., Nealis, V.G., Taylor, S.W., 2010. Potential for range expansion of mountain pine beetle into the boreal forest of North America. The Canadian Entomologist 142, 415–442.
Schaalge, G.B., van der Vaart, H.R., 1988. Relationships among recent models for insect population dynamics with variable rates of development. In: McDonald, L., Manly, B, Lockwood, J., Logan, J. (Eds.), Estimation and analysis of insect populations, vol. 55. Lecture Notes in Statistics, pp. 299–312.
Schoolfield, R.M., Sharpe, P.J.H., Magnuson, C.E., 1981. Non-linear regression of biological temperature-dependent rate models based on absolute reaction-rate theory. Journal of Theoretical Biology 88, 719–731.
Schwartz, M.D., 1998. Green-wave phenology. Nature 394, 839–840.
Sharpe, P.J.H., DeMichele, D.W., 1977. Reaction kinetics of poikilotherm development. Journal of Theoretical Biology 64, 649–670.
Sharpe, P.J.H., Curry, G.L., DeMichele, D.W., Cole, C.L., 1977. Distribution model of organism development times. Journal of Theoretical Biology 66, 21–38.
Smerage, G.H., 1988. Models of development in insect populations. In: McDonald, L., Manly, B., Lockwood, J., Logan, J. (Eds.), Estimation and analysis of insect populations, vol. 55. Lecture Notes in Statistics, pp. 313–331.
Sparks, T.H., Carey, P.D., 1995. The responses of species to climate over two centuries: an analysis of the Marsham phenological record, 1736–1947. Journal of Ecology 83, 321–329.
Stinner, R.E., Butler Jr, G.D., Bacheler, J.S., Tuttle, C., 1975. Simulation of temperature-dependent development in population dynamics models. The Canadian Entomologist 107, 1167–1174.
Taylor, F., 1981. Ecology and evolution of physiological time in insects. The American Naturalist 117, 1–23.
van Straalen, N.M., 1983. Physiological time and time invariance. Journal of Theoretical Biology 104, 349–357.
Visser, M.E., Both, C., 2005. Shifts in phenology due to global climate change: the need for a yardstick. Proceedings of the Royal Society B 272, 2561–2569.
Wagner, T.L., Olson, R.L., Willer, J.L., 1991. Modeling arthropod development time. Journal of Agricultural Entomology 8, 251–270.
Wagner, T.L., Wu, H., Sharpe, P.J.H., Coulson, R.N., 1984. Modeling distributions of insect development time: a literature review and application of the Weibull function. Annals of the Entomological Society of America 77, 475–483.
Wang, E., Engel, T., 1998. Simulation of phenological development of wheat crops. Agricultural Systems 58, 1–24.
Weber, J.D., Volney, W.J.A., Spence, J.R., 1999. Intrinsic development rate of spruce budworm (Lepidoptera: Tortricidae) across a gradient of latitude. Environmental Entomology 28, 224–232.
Worner, S.P., 1991. Use of models in applied entomology: the need for perspective. Environmental Entomology 20, 768–773.
Worner, S.P., 1992. Performance of phenological models under variable temperature regimes: consequences of the Kaufmann or rate summation effect. Environmental Entomology 21, 689–699.
Yang, L.H., Rudolf, V.H.W., 2010. Phenology, ontogeny and the effects of climate change on the timing of species interactions. Ecology Letters 13, 1–10.
Yurk, B.P., Powell, J.A., 2010. Modeling the effects of developmental variation on insect phenology. Bulletin of Mathematical Biology 76, 1334–1360.