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

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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 eV$^{-1}$ is a near-constant activation energy, and $k = 8.6173 \times 10^{-5}$ eV K$^{-1}$ is the Boltzmann constant relating energy to temperature, $K(\text{eV})$. 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...
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; Schaalje 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 their 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 characterizing 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 Bactrocerca cucurbitae (Coqillet) (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 development time. Development time and rate are related by:

$$\tau(T, A) = \frac{1}{r(T, A)}$$  \hspace{1cm} (1)

where $\tau(T, A)$ represents the modeled average time required to complete the life stage at temperature $T$, and $A$ is a vector of parameter values of temperature-response function $r(T, A)$. To model development under fluctuating temperature regimes, it is necessary to sum (integrate) development rates over short time steps, $\Delta t$, 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):

$$a_i = \int_0^{t_i} r(T, A) \, dt \approx \sum_0^i r(T, A) \, \Delta t.$$  \hspace{1cm} (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 $t_i$ 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 $t_i \neq \tau(T, A)$. 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, $\tau(T, A)$, and the true mean (or expected) development time, $E(t_i)$. If we define an individual’s deviation from $E(t_i)$ as $\delta_i$, and the lack-of-fit between theoretical and treatment mean, $v_j$, we get:

$$t_i = \delta_i + v_j \tau(T, A).$$  \hspace{1cm} (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 $\delta \geq 0$, which is consistent with the fact that rates can only be $\geq 0$ 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 $e$ is normally-distributed then $\delta = e^\delta$ and $1/\delta = e^{-\delta}$ are both lognormally-distributed), the error structure is the same whether variability is expressed as development times or development rates. Thus:

$$e_{ij} = \ln(t_{ij}/[n_j \tau(T, A)])$$  \hspace{1cm} (4)

is a normally-distributed random variable with mean $\mu_{eij} = -1/2\sigma_{\delta}^2$ and variance $\sigma_{eij}^2$ (the skew of the lognormal distribution requires a non-zero $\mu_{eij}$, 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, $v_j = E(t_i)/\tau(T, A)$,

$$v_j = E(t_i)/\tau(T, A).$$  \hspace{1cm} (5)

can be assumed to be a multiplicative normally-distributed random effect with mean 1 and variance $\sigma_{v_j}^2$ that is random with respect to treatment.
Table 1

Selected temperature-dependent development rate equations.

<table>
<thead>
<tr>
<th>Formulation</th>
<th>Validity range</th>
<th>Parameters</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>(A1) ( r(T) = \exp \left[ \frac{E}{T - T_m} \right] )</td>
<td>( T &gt; -273 )</td>
<td>3</td>
<td>Taylor (1981)</td>
</tr>
<tr>
<td>(A2) ( r(T) = \phi (T, T_m) )</td>
<td>( T_0 &lt; T &lt; T_m )</td>
<td>4</td>
<td>Brière et al. (1999)</td>
</tr>
<tr>
<td>(A3) ( r(T) = \frac{1}{(T - T_m)^{1/2}} )</td>
<td>( T_0 &lt; T &lt; T_m )</td>
<td>4</td>
<td>Wang and Engel (1998)</td>
</tr>
<tr>
<td>(A4) ( r(T) = \phi \left( \frac{\ln(T - T_m)}{T - T_m} \right) )</td>
<td>( T_0 &lt; T &lt; T_m )</td>
<td>4</td>
<td>Hilbert and Logan (1983)</td>
</tr>
<tr>
<td>(A5) ( r(T) = \phi \left( \frac{\ln(T - T_m)}{T - T_m} \right) + \phi \left( \frac{\ln(T - T_m)}{T - T_m} \right) )</td>
<td>( T_0 &lt; T &lt; T_m )</td>
<td>5</td>
<td>Hansen et al. (2011)</td>
</tr>
<tr>
<td>(A6) ( r(T) = \phi \left( \frac{\ln(T - T_m)}{T - T_m} \right) + \phi \left( \frac{\ln(T - T_m)}{T - T_m} \right) )</td>
<td>( T_0 &lt; T &lt; T_m )</td>
<td>6</td>
<td>This paper</td>
</tr>
<tr>
<td>(A7) ( r(T) = \frac{\mu e^{\frac{\mu}{T - T_m}}}{1 + e^{\frac{\mu}{T - T_m}}} )</td>
<td>( T &gt; -273 )</td>
<td>6</td>
<td>Schoofield et al. (1981)</td>
</tr>
</tbody>
</table>

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:

\[
q_{ij}(\sigma_c, \sigma_v, \textbf{A}) = f(t_j) \left\{ F \left[ \ln \left( \frac{t}{t_j(T_j, \textbf{A})} \right) \right] - F \left[ \ln \left( \frac{t - dt}{t_j(T_j, \textbf{A})} \right) \right] \right\},
\]

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

\[
\text{LL}(\sigma_c, \sigma_v, \textbf{A}) = -\sum_i \sum_j \ln[q_{ij}(\sigma_c, \sigma_v, \textbf{A})].
\]

The set of parameter values \( \textbf{A}, \sigma_c \), and \( \sigma_v \) that minimize LL can be found through iterative optimization routines such as Procedure NLMMIXED of SAS (see Appendix A for suggested SAS code). While the details of Eq. (6) are specific to the normal distribution assumed for \( v \) and the lognormal distribution for \( \sigma \) (see Eq. (4)), its general form (probability of a value of \( v \) times the difference in cumulative probabilities of \( \sigma \) 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.

2.3.2. 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 derhave, 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 \( (T_i) \) for a fixed amount of time \( (t_i) \); short enough to avoid excessive mortality but long enough for significant development to occur, and then transferred to another temperature \( (T_j) \) to record the time \( t_{ij} \) required by individual \( i \) to complete the stage under more optimal conditions. For individuals involved in such transfer treatments, development is complete when:

\[
\frac{t_{1j}}{t_{1j}} + \frac{t_{2j}}{t_{2j}} = 1.
\]

By rearranging (11), we get:

\[
ev_i = \ln \left( \frac{t_{1j}}{t_{1j}} + \frac{t_{2j}}{t_{2j}} \right).
\]

and Eq. (6) becomes

\[
q_{ij}(\sigma_c, \sigma_v, \textbf{A}) = f(t_j) \left\{ F \left[ \ln \left( \frac{t_{1j}}{t_{1j}} + \frac{t_{2j}}{t_{2j}} \right) \right] - F \left[ \ln \left( \frac{t_{1j}}{t_{1j}} + \frac{t_{2j}}{t_{2j}} \right) \right] \right\},
\]

where \( F \) is the cumulative normal probability distribution with variance \( \sigma_v^2 \) and mean \(-1/2\sigma_v^2 \) and \( f \) is the normal probability density.
function with variance \( \sigma_0^2 \) and mean 1. Note that Eq. (6) is a special case of Eq. (13) where \( \delta_j = 0 \) (no transfer treatment), and that Eq. (13) can represent the \( q_{ijk}(s_1, s_2, A) \) term in Eq. (8) to estimate the parameter set \( A, \sigma_1, \) and \( \sigma_2 \), 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 (\( t_i \)) and their associated sample sizes (\( n_i \)) 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:

\[
i_j = \delta_j \tau_i(T_j, A)
\]

where \( \delta_j = \sum \delta_{ji}/n_i \). While \( \delta_j \) are lognormally distributed, their mean is approximately normally distributed because of the central limit theorem and we get:

\[
\delta_j = \frac{t_j}{n_j \tau(T_j, A)} \sim N \left( 1, \frac{\sigma_j^2}{n_j} \right)
\]

with \( t_j \sim N(1, \sigma_j^2) \). When treatment \( j \) involves a temperature transfer from \( T_{ij} \) for \( t_{ij} \) days, to temperature \( T_{ij} \) for the remainder of development (averaging \( t_{ij} \)), this becomes:

\[
i_j = \frac{t_{ij}}{n_j \tau(T_j, A)} + \frac{t_{ij}}{n_j \tau(T_j, A)}.
\]

The probability of observing mean development time \( \tilde{t}_j \) (or \( \tilde{t}_{ij} \)) with temperature transfer is:

\[
q_j(\sigma_j, s_1, A) = f(t_j)/f(\delta_j)
\]

where \( f(t_j) \) is the normal probability density function, with mean 1 and variance \( \sigma_j^2 \) or \( \sigma_j^2/n \). The negative log likelihood to be minimized is:

\[
LL(\sigma_j, s_1, A) = -\sum_j \ln(q_j(\sigma_j, s_1, A))
\]

(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 \( \sigma_j^2 = e^{\varepsilon^2} - 1 \), we get:

\[
\sigma_j^2 = \ln(\sigma_j^2 + 1)
\]

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, \( i_j \), of their remaining fecundity, \( F_i \), per unit of time. This proportion can be a function of temperature, \( \lambda(T, B) \), with set of parameters \( B \). Under these assumptions, the oviposition rate is:

\[
\frac{dF_i}{dt} = -\lambda(T, B)F_i.
\]

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 \( F_i = F_0 e^{-\lambda(T, B)(-t_0)} \), where \( F_0 \) is mean (potential) fecundity. We also assume lognormal variation in fecundity so that an individual's initial fecundity is \( n_{ij} = e^\varepsilon \), where \( e^\varepsilon \sim N(\ln(F_0) - 1/2\sigma_0^2, \sigma_0^2) \). In many experiments, the number of eggs laid is measured on several occasions, indexed \( k \), for each female throughout the interval \( [t_0 - 1, t_1] \). The expected oviposition by individual \( ij \) during that interval is:

\[
O_{ijk} = n_{ijk}e^{-\lambda(T_j, B)\varepsilon(t_1 - t_0)} - e^{-\lambda(T_j, B)\varepsilon(t_0 - t_0)}
\]

for \( t \geq t_0 \). Parameters \( F_0, \sigma_0 \), and \( B \) 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 \( E_{ijk} \):

\[
q_{ijk}(\sigma_j, B) = f(e_j) = \frac{e_j^{E_{ijk}} e^{-O_{ijk}}}{E_{ijk}!},
\]

where \( f \) is the normal probability density function with variance \( \sigma_j^2 \) and mean \( \ln(F_0) - 1/2\sigma_0^2 \). The negative log likelihood to be minimized is:

\[
LL(\sigma_j, B) = -\sum_j \sum_k \sum_i \ln[q_{ijk}(\sigma_j, B)].
\]

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, \( \gamma(T_j, C) \), where \( C \) is a vector of parameter values. Survival over the duration of a given life stage in treatment \( j \) is:

\[
S_j = \gamma(T_j, C)^{t_j},
\]

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

\[
S_j = \gamma(T_1, C)^{t_1} \gamma(T_2, C)^{t_2},
\]

with temperatures \( T_1 \) and \( T_2 \) for times \( t_1 \) and \( t_2 \) 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 \( n_j k_j \). The negative log likelihood to be minimized is:

\[
LL(C) = -\sum_j \ln[n_j k_j e^{-n_j k_j}]/k_j!.
\]

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

\[
S_t = \prod_t \gamma(T_t, C)^{\Delta t},
\]

where \( \Delta t \) 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 (\( \tilde{t}_j \)) in Eq. (24) by the stage's developmental response function (Eq. (1)):

\[
S = \gamma(T, C)^{\tau(T, A)}.
\]

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 $A = (T_2 = 5, A_2 = 0.1, T_m = 33, A_m = 3, \omega = 0.13, \psi = 0.01, \sigma_2 = 0.15$ and $\sigma_1 = 0.1$. This function includes explicitly two developmental thresholds and their respective boundary regions ($T_m, A_m$; lower; $T_2, A_2$; upper). At temperatures $T = (4, 8, 12, 16, 20, 24, 28, 32 \degree C)$, we applied lack-of-fit error by drawing values of $v \in N(1, \sigma^2)$ at random. This yielded three stochastically different mean development times $\mu(T)$ for each temperature. From each mean, we drew a sample of 50 random values of $v \sim N(-1/2A_2^2, \sigma^2)$ to obtain $\delta = \epsilon^{v}$ 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 $t = \text{round}[\delta \exp(T, A) + 0.5]$.

These data constituted the first “experiment”; censoring was applied to individuals with development times $>75$ days. No individuals at $4 \degree C$ completed development prior to censoring and only a few were censored at $8 \degree C$. In a second experiment, individuals were transferred to $T_2 = 16 \degree C$ after $t_1 = 30$ days at $4 \degree C$, $t_1 = 20$ days at $T_1 = 8 \degree C$ or $t_1 = 6$ days at $T_1 = 32 \degree C$. No censoring was applied. The time required to complete development at $16 \degree C$ 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 $j$ surviving to the end of its development is $P_{\text{survival}}(j) = s^T$ for individuals kept at constant temperature. $P_{\text{survival}}(j) = s^T$ for censored observations ($c = 75$ in our example), and $P_{\text{survival}}(j) = s^T$ for those in transfer treatments. The fate of individuals (survival or not) was set by drawing a uniformly distributed random number $\xi$ in the range $[0,1]$ for each and using $\xi < P_{\text{survival}}(j)$ 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 $28.0 \pm 1 \degree C$). Egg masses were kept for 28–31 days at either 4.7 or $8.7 \degree C$, and then transferred to $15.6 \degree C$ to hatch. Sample sizes ranged from 19 to 24 egg masses per temperature, except in the $4.7 \degree C$ 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 or $30 \degree C$ for 30 days then transferred to $15.8 \degree C$ to complete development ($n = 34$) or were kept at $15.8 \degree C$ throughout ($n = 33$). Only 4/34 egg masses in this additional transfer treatment hatched, compared to 30/33 of those kept at $15.8 \degree C$. 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 $31.9 \degree C$), plus two transfer treatments (32 or 38 days at $T_1 = 7.6 \degree C$, with development completed at $T_2 = 19.5 \degree C$). 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 (e.g., 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 $15 \times 15 \text{cm}$ phloem sections wounded 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 (Perctival Scientific, Inc., Gray et al., 1998) at constant temperatures ranging from 4 to 27.5 $\degree C$. Larval moths 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 $20 \degree C$ 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 (A6)). 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 $\degree C$ (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 $\degree C$. 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 $\degree C$. Both datasets consist of the number of individuals reared and surviving, and the average development time at each temperature $T$ (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 $\gamma(T, C) = 1/(1 + \exp(a + bT + cT^2 + dT^3 + eT^4))$ 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 $v_i \in N(1, \sigma^2)$ associated with population $k$ so that $\gamma(T, C) = 1/(1 + \exp(a + bT + cT^2) + v_k)$ in Eq. (24).
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 \(T \), 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 \(>8^\circ C\). 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 \(^\circ C\) allowed the model to estimate a much more realistic lower threshold of \(T_l = 278.3 ± 0.7 K (5.3 ^\circ C\) compared with the “true” value of 5 \( ^\circ C\) (inset, Fig. 1b). The upper threshold, beyond which development rates drop sharply, was estimated well with all three datasets at \(T_h = 303.1 \pm 0.3 K (30.1-30.2 ^\circ C)\). Estimates of variances were close to the true values in all cases. The maximum likelihood method estimated \(\sigma_q = 0.153\) to 0.159 and \(\sigma_r = 0.075\) to 0.077 compared with the “true” values of \(\sigma_q = 0.15\) and \(\sigma_r = 0.1\).

4.2. Western spruce budworm and spruce budmoth egg development

Western spruce budworm and spruce budmoth 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 \(^\circ C\)) and 15.6 or 15.8 \(^\circ C\). 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 \(\sigma_q\). However, the lack-of-fit term \(\sigma_q\) varied considerably and was lowest with the best-fitting model (Fig. 3a), a relationship that illustrates the importance of including lack-of-fit variance \(\sigma_q\) so that the estimate of individual variation \(\sigma_q\) 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 \(\rho_{25} = 0.117\) ±

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<thead>
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<th>Censored at 75 days</th>
<th>With transfers</th>
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<td>0.119 ± 0.004</td>
<td>0.121 ± 0.004</td>
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<tr>
<td>(H_a)</td>
<td>19764 ± 978</td>
<td>19764 ± 867</td>
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<tr>
<td>(H_l)</td>
<td>-60000 ± 9</td>
<td>-60000 ± 7</td>
<td>-60000 ± 27</td>
</tr>
<tr>
<td>(T_l)</td>
<td>265.6 ± 104.9</td>
<td>272.1 ± 5.6</td>
<td>278.3 ± 0.7</td>
</tr>
<tr>
<td>(T_h)</td>
<td>100017 ± 34</td>
<td>100017 ± 28</td>
<td>100017 ± 36</td>
</tr>
<tr>
<td>(\sigma_q)</td>
<td>0.153</td>
<td>0.155</td>
<td>0.159</td>
</tr>
<tr>
<td>(\sigma_r)</td>
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<td>0.077 ± 0.014</td>
<td>0.075 ± 0.015</td>
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<tr>
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<td>272.1 ± 5.6</td>
<td>278.3 ± 0.7</td>
</tr>
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</tr>
<tr>
<td>AICc</td>
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<td>213.4</td>
<td>213.4</td>
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</table>

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.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>(A1)</th>
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<th>(A3)</th>
<th>(A4)</th>
<th>(A5)</th>
<th>(A6)</th>
<th>(A7)</th>
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<td>(T_r = 5.5)</td>
<td>(T_r = 5)</td>
<td>(T_r = 2.0)</td>
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<td>2</td>
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<td>(T_m = 41.5)</td>
<td>(T_m = 39.8)</td>
<td>(T_m = 43.0)</td>
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<tr>
<td>3</td>
<td>(\psi = 0.19)</td>
<td>(\omega = 0.643)</td>
<td>(T_r = 30.0)</td>
<td>(A_n = 47.8)</td>
<td>(A_n = 5.9)</td>
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<td>4</td>
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<td>5</td>
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<td>(\psi = 0.0231)</td>
<td>(\omega = 0.109)</td>
<td>(T_m = 308.22)</td>
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<td>(T_r = 0.0231)</td>
<td>(\rho_{25} = 0.0469)</td>
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0.012, \( H_a = 13476 \pm 2176 \), \( H_t = -60076 \pm 144 \), \( T_l = 279.7 \pm 1.2^\circ K \), \( H_a = 59946 \pm 81 \), \( T_l = 303.8 \pm 3.0^\circ K \) and a small amount of lack-of-fit variation \( \sigma^2 \approx 0.03 \). From the mean development times and sample sizes, we estimated \( \sigma = 0.36 \), or \( \sigma = 0.12 \) (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 \(^\circ C\) compared very well with the measurements obtained from insects kept at 7.6 \(^\circ C\) 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 \( \sigma \), but there was a very definite one with the lack-of-fit term \( \rho_s \) (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, h, j and k; Tables 4 and 5). It is in the fourth instar that the lower development threshold was highest (\( T_b = 16.2 \) \(^\circ C\); \( D_b = 0.04 \) \(^\circ C\)), 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 \(^\circ C\) 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 \(^\circ C\) (Fig. 4s) which led to threshold estimates of \( T_a = 4.2 \) \(^\circ C\) (\( D_a = 0.1 \) \(^\circ C\)) and \( T_m = 35 \) \(^\circ C\) (\( A_m = 7.2 \) \(^\circ C\); Fig. 4t). This emergence response differs from an adult flight threshold in the field which is estimated to be approximately 15.5 \(^\circ C\) (Reid, 1962). Oviposition occurred at temperatures as low as 7 \(^\circ C\) and the upper threshold was estimated at \( T_m = 27.7 \) \(^\circ C\) (\( A_m = 3.1 \) \(^\circ C\); 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 \(^\circ C\) (Fig. 4v).

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:

\[
S_j = \left( \frac{1}{1 + e^{bx+ct^2+dt^3+et^4}} \right)^{1/ \rho_s}, \tag{29}
\]

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 \( \rho_s = 1.006 \pm 0.039 \), \( H_a = \]
Fig. 3. Relationship between log likelihood (goodness of fit) and the $\sigma_i$ and $\sigma_j$ terms in Eq. (3) obtained by fitting various models to (a) western spruce budworm and (b) mountain pine beetle egg development. The estimates of $\sigma_i$, the individual variation in development times, are stable from model to model, while the value of $\sigma_j$, the lack-of-fit term, appropriately increases as negative log likelihood increases.

6609 ± 1156, $H_T = -41826 ± 1622$, $T_1 = 289.8 ± 0.8^\circ$K, $H_N = 147580 ± 9190$, $T_N = 309.0 ± 0.1^\circ$K, with $\sigma_S = 0.238 ± 0.036$.

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,

$$S_j = \frac{1}{1 + e^{a+bt+cT^2}} + y_k$$

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 ($\sigma_s = 0.00189 ± 0.00106$, $t_5 = 1.79$, $P = 0.13$). 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 near 30°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>
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<tr>
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</tbody>
</table>
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

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**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 $\eta$. 

---

Note: The image contains graphs and data tables that are not transcribed here due to the limitations of text-only representation.
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 $\sigma_c^2$ 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
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 α 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/δ 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 b₀ 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

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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

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 = s_eps**2 + (1 + s_upsilon**2) + s_upsilon**2;
   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 T1 (temperature transfers in the design);
   tk1 = T1 + 273;
   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));
   tpred2 = upsilon * tau;
   Development time at T2 (temperature transfers in the design);
   tk2 = T2 + 273;
   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) -
      (1-censored) * (1-cdf('normal',epsij,se2,s_eps));
   ll = log(p);
   if(p > 1e-10) then ll = log(p);
   else ll = log(1e-10);
   model epsij ~ general(n + ll);
   random upsilon ~ NORMAL(1.0,s_upsilon,s_upsilon)
   subject = T1;
run;

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

data Weber_et_al_1999;
   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
      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
      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
      5 9.3 6 97.3 7 17
      5 11.2 2 73.5 3 12
      (continued on next page)
proc sort data=Weber_et_al_1999;
   by pop T;
run;

persona;      /C24

\begin{verbatim}
/* Sharpe-Schofield Eq. (A7)*/
TK = T + 273;
num = rho25 * TK/298 * EXP(HA/1.987 + (1/TL-1/TK));
den1 = EXP(1/TL-1/TK);
den2 = EXP(HH/1.987 + (1/TH-1/TK));
tau = 1/(num/(1 + den1 + den2));
if(upon > 0) then delta_bar = time/(upon + tau);
else delta_bar = 1000; /*Some non-sensical value*/
model delta_bar ~ normal(1_s_delta + s_delta/n);
random upson ~ normal(1_s_upson + s_upson)
subject = Pop;
run;
\end{verbatim}

References

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.


